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TAXONOMY AND ECOLOGY OF THE PROPAGULIFEROUS SPECIES OF *POHLIA* HEDW. (MUSCI) IN NORTH AMERICA

by

© Arthur Jonathan Shaw

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

DEPARTMENT ....Botany................

EDMONTON, ALBERTA
SPRING, 1980

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Taxonomy and ecology of the propaguliferous species of *Pohlia* Hedw. (Musci) in North America

submitted by Arthur Jonathan Shaw

in partial fulfilment of the requirements for the degree of Master of Science

Dale H. Vitt
Supervisor

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Date 19 Feb 1980

ABSTRACT

The genus *Pohlia* is represented by about 29 species in North America. The most recent revision of *Pohlia* in North America recognized six species in the section *Pohliella* which are characterized by asexual, axillary propagula produced in the leaf axils of sterile, and rarely fertile gametophytic shoots. The geographic distribution of these taxa has been inadequately investigated because of taxonomic and nomenclatural problems surrounding them. Species of this propaguliferous complex are notably uniform in most sporophytic features such as exostome and endostome morphology, exothecial cell pattern and annulus morphology, and this group probably represents a monophyletic assemblage. Nine North American species are recognized, and each can be best defined on the basis of the developmental pathway which characterizes its propagula. Because of their similarity in position, appearance, and manner of development, these propagula are considered homologous with axillary branches. A continual gradient of structural complexity exists between propagula of different species, and is interpreted as a reduction series. Evolutionary reduction in propagulum complexity probably occurred through progressive modification of ontogenetic pathways.

Two species, *Pohlia tundrae* and *P. andrewsii*, are

described as new to science, and *P. camptotrachela* (Ren. & Card.) Broth. is considered distinct from its closest living relative, *P. annotina* (Hedw.) Lindb. A study of the nomenclatural history of these propaguliferous species indicates that the name *P. rothii* (Corr. *ex* Limpr.) Broth. should be considered synonymous with *P. filum* (Schimper) Mart., and *P. annotina* (Hedw.) Lindb. is the earliest valid name for the taxon described by Hedwig (1801) as *Bryum annotinum*. The combination *Pohlia andalusica* (Höhn.) Broth. is the earliest name for the taxon most recent authors have referred to as *P. rothii*.

Each species of the propaguliferous complex has a distinct geographic distribution in North America, and occupies a characteristic and narrowly defined range of edaphic conditions. The complex as a whole can be characterized as mildly acidophilic, but species behave individualistically in relation to soil pH. In western North America, the propaguliferous species occur primarily in three habitats; roadbanks, tundra, and bare sand or gravel, and these habitats can be characterized quantitatively by the amount of organic matter present in each. With the exception of *P. tundrae* and *P. drummondii*, each species was found to be statistically distinct from every other species along the pH gradient, the organic matter gradient, or both. Ecological data correlates with the inferred direction of structural evolution in this group, and indicates that the direction of ecological evolution has been from soil of high organic matter content and intermediate pH to soil of low organic matter content and either high or low pH.

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I wish to thank Dale H. Vitt for his supervision and advice concerning all facets of this research and for critically reviewing this manuscript. My gratitude is also extended to M. Hickman, G. Ball and K. Denford for providing critical reviews of the manuscript. I am grateful to E. Nyholm and A.C. Crundwell for discussing various taxonomic problems, and for arranging loans of herbarium specimens. A special thanks goes to P. Isoviita for arranging loans of herbarium material and for providing information, advice and insight into many nomenclatural problems in *Pohlia*. I am grateful to the following persons for arranging herbarium loans from their respective institutions: L.E. Anderson, C.D. Bird, G.R. Brassard, W. Buck, S. Churchill, M.R. Crosby, H. Crum, M. Denton, E. Lawton, S.R. Edwards, D. Engelmark, P. Geissler, O. Gjaerevoll, S.R. Gradstein, D. Griffin, A.J. Harrington, S.G. Harrison, F. Hermann, H. Hertel, R.R. Ireland, H. Kasaki, H. Krog, W.F. Mahler, E. McClintock, K. Mecenovic, G.S. Mogensen, B. Murray, H. Nowak, R. Ornduff, D. Pfister, R.A. Pursell, M. Rajczy, P.L. Redfearn, W.D. Reese, H. Robinson, W.B. Schofield, A.J. Sharp, E. Urmi, G. Wagenitz, W. Weber, and C.M. Wetmore. I also thank Susan Hamilton for typing this manuscript and for assisting in many details of format.

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INTRODUCTION

The moss genus *Pohlia*, a member of the large family Bryaceae, consists of approximately 85 species (117 according to Brotherus 1924) distributed throughout the world, but with the greatest diversity in temperate regions of the northern hemisphere. In North America, *Pohlia* is represented by about 29 species (26 according to Andrews 1935, excluding *Epipterygium tozeri* Lindb. and *Anomobryum filiforme* Husn.) which range from subtropical Florida to arctic Alaska and the Canadian arctic archipelago.

In North America, a group of nine dioicous *Pohlia* species in the section *Pohliella* are characterized by asexual propagula produced in the leaf axils of sterile (and rarely fertile) gametophytic shoots. These species are listed below in comparison to the citations given by Andrews (1935) in his most recent revision of the genus in North America.

	Andrews 1935
Pohlia drummondii (C. Müll.) Andr.	*P. drummondii* (C. Müll.) Andr.
P. filum (Schimp.) Mårt.	*P. gracilis* (Schleich.) Lindb.
P. andalusica (Höhn.) Broth.	*P. rothii* (Corr.) Broth. (*ex*. part)
P. tundrae J. Shaw	
P. bulbifera (Warnst.)Warnst.	*P. bulbifera* (Warnst.)Warnst.
P. annotina (Hedw.) Lindb.	*P. annotina* (Hedw.) Loeske
P. proligera (Lindb. *ex* Breidl.) Lindb. *ex* Arn.	*P. proligera* Lindb.
P. camptotrachela (Ren. & Card.) Broth.	(Treated as synonym of *P. annotina*)
P. andrewsii J. Shaw	

In the present work, the asexual axillary structures characteristic of this group of *Pohlia* species are referred to as propagula, these same propagula being called gemmae by Andrews (1935) and Nyholm (1958), brood bodies by Crum (1976) or bulbils by Lewis and Smith (1977, 1978). Each of the nine propaguliferous Pohlias in North America consistently produces propagula, although in number these can range from one or a few to over 100 per shoot. The propagula consist of a simple to more or less differentiated propagulum body, and one to five or six, usually apical, leaf primordia. In the present work, the leaf primordia are interpreted as being homologous with the leaf primordia of young branch buds, and the propagula to the buds themselves. The reasons for this interpretation, together with a detailed discussion of propagulum morphology, are given in a later section.

The propaguliferous *Pohlia* species in the section *Pohliella* are typically soil growing mosses, as are most members of the Bryaceae, and include wide-ranging lowland-montane species (e.g. *P. annotina*),alpine species largely restricted to tundra habitats (e.g. *P. tundrae*),and one species recorded only from arctic regions (*P. andrewsii*). All nine species occur in western North America where they are frequent in mountainous areas wherever the bedrock is not highly calcareous. Several species (*P. annotina*, *P. andalusica*, *P. bulbifera*, *P. proligera*, *P. drummondii*) also occur in eastern North America, but only *P. annotina* extends farther south than New York and New England. None of the species is entirely restricted to eastern North America. Specimens of all species except *P. tundrae* have been seen from Europe, and this species may be endemic to western North America.

Species of this group of propaguliferous Pohlias are very similar to one another in such features as general gametophytic habit, leaf and leaf cell size and shape, exostome and endostome morphology, exothecial cell pattern, and annulus morphology. These characters are thought to provide reliable specific and subgeneric distinguishing criteria within *Pohlia*, and the notable uniformity of the propaguliferous species is probably indicative of close phylogenetic relations between species and a monophyletic origin for the complex. The species are distinguished mainly by differences in the size, shape, number and degree of differentiation of their propagula, although they also differ in leaf sheen, pigmentation, stature and other subtle gametophytic features and in most cases, species are recognizable even in the absence of propagula. There are other members of the genus *Pohlia* which are similar to the propaguliferous species in many morphological features, and these are undoubtedly related to the propaguliferous complex (e.g. see Nyholm 1958). These nonpropaguliferous species, however, are not included in the present revision.

THE OCCURRENCE OF PROPAGULA IN THE BRYACEAE

Asexual propagula are quite common in the class Bryopsida, where they are frequent among both the mosses and the liverworts. Correns' (1899) treatise is the most thorough review of asexual reproduction among mosses to date. Goebel (1930) discussed asexual reproduction in selected moss taxa, and Watson (1964) provided a review of asexual reproduction and its ecological significance in bryophytes. Whitehouse (1966) surveyed the British moss flora for the occurrence of rhizoidal propagula, and many other publications deal with asexual reproduction in specific moss groups (e.g. Heald 1898, Plitt 1909, Lowry and Steere 1946, Welch 1948, Crundwell and Nyholm 1963, Frederick and Ward 1968, Whitehouse 1969, Delgadillo and Sharp 1976, Crundwell et al 1978).

Within the Bryaceae, the occurrence of propagula is found in many unrelated taxa. Some species, for example, *Bryum alpinum* Brid. (Crundwell and Nyholm 1964), produce rhizoidal propagula, but are unrelated to other species which produce similar structures. *Brachymenium exile* (Dozy & Molk.) Bosch. & Lac. (Ochi 1959) is another species which produces propagula, but is not part of a larger propaguliferous complex. In these cases, the origin of propagula probably occurred independently, and was not followed by the evolutionary divergence of closely related species differing in the form of their propagula.

On the other hand, there also exists within the Bryaceae, groups of asexually reproducing species which are uniform sporophytically, differing only or mainly in the form of their propagula (cf. the present group of propaguliferous Pohlias). In the genus *Bryum*, the *B. erythrocarpum* complex (Crundwell and Nyholm 1964) is an example of the latter situation in which a group of closely related species produce morphologically similar propagula. Crundwell and Nyholm (1964) recognized nine European members of this group, saying that the species are very similar morphologically, and that they have found the propagula to be so important in the recognition of species that they did not attempt to determine collections in which they are absent.

The *Bryum bicolor* group, recently studied in Europe by Wilczek and Demaret (1976) and Smith and Whitehouse (1978), represents another complex of morphologically similar, closely related species. Smith and Whitehouse (1978) found that sporophyte morphology is uniform within the group, and that differences in leaf and propagulum morphology are the most useful taxonomic characters for distinguishing the four British species of that complex. In the *B. bicolor* group, as in the present propaguliferous Pohlias, the propagula differ in the size and complexity of the body, and in the degree of differentiation of the leaf primordia (Smith and Whitehouse 1978).

Syed (1973) recently revised *Bryum capillare* Hedw. and related species, and found that the "aggregate species" recognized by Hedwig (1801) can be divided into eleven consistently recognizable species on the basis of propagulum morphology and other gametophytic features.

The *Bryum erythrocarpum* complex, *B. capillare* and related species, and the *B. bicolor* group are similar to the propaguliferous Pohlias in the morphological uniformity of sporophytes and many gametophytic features within the groups, and most likely each represents a monophyletic assemblage of species which have diverged mainly in the form of their propagula. Each of them shares the reputation of being "taxonomically difficult groups", this being the result of seemingly continuous variation in the morphology of the propagula. In this respect, these groups can be said to consist of assemblages of "micro-species", in the same sense that such assemblages exist in many asexually reproducing vascular plants (cf. e.g. Grant 1971).

The genus *Pseudopohlia*, which is closely related to *Pohlia*, consists of yet another group of Bryaceous mosses in which the species differ mainly in the form of their propagula. There are presently three species included in *Pseudopohlia* (by Van der Wijk et al 1967); *P. bulbifera* Williams, *P. didymodontia* (Mitt.) Andr., and *P. yunnanensis* Herz., although Andrews (1950) suggested that perhaps

P. bulbifera and *P. didymodontia* may best be considered a single taxon, but need further study. This propaguliferous complex is definitely in need of taxonomic revision in conjunction with culture studies of living plants.

Within the genus *Pohlia*, there are several groups of species characterized by the production of asexual, axillary propagula. The *Pohlia flexuosa* group consists of approximately 2-5 poorly understood species which occur primarily in tropical latitudes (Andrews 1950, Ochi 1959). Like other propaguliferous groups of species in the Bryaceae, species of the *P. flexuosa* complex are morphologically similar but differ in the form of their propagula. As the propagula are sometimes very similar to those of the northern latitude species in the section *Pohliella*, it was thought that perhaps the *P. flexuosa* group should be phylogenetically interpreted as belonging to the propaguliferous complex in *Pohliella*. However, members of the *P. flexuosa* group differ from the northern latitude species in a number of important features. Gametophytically, *P. flexuosa* and related species are considerably more freely branching than any of the propaguliferous species of the section *Pohliella*, and unlike the latter species, members of the *P. flexuosa* group have moderately to strongly incrassate leaf cells. Further, *P. flexuosa* and related species differ from members of the section *Pohliella* in several, definitive sporophytic features. The exothecial cells are unlike the rectangular, sinuose-walled cells of the "*Pohliella* species", and in the *P. flexuosa* group they are often conspicuously bulging, a character state absent from any species of North American *Pohlia*. Finally, the peristome of *P. flexuosa* and related species is unlike any of the propaguliferous species in *Pohliella* in being white (both exostome and endostome), and in being completely devoid of cilia. The exostome teeth are more blunt than those of the species in *Pohliella*, and the external sculpturing is more coarse and extends more continuously to the base of the tooth. The endostome segments, unlike the northern species, are only narrowly perforate. It is consequently concluded that propagula of the *P. flexuosa* group have arisen independently of those of species in the section *Pohliella*, and represent a striking case of convergence in propagulum morphology.

Vitt (1971) described *Pohlia ochii* from Campbell Island, New Zealand, and reported the occurrence of linear, vermicular propagula in the upper leaf axils. Sporophytes of *P. ochii* are unknown, but the simple, unbranched stems and the glossy-leaves with thin walled cells are more reminiscent of the northern latitude species than of the *P. flexuosa* group; however the affinities of *P. ochii* must await the discovery of sporophytes.

Elsewhere in the genus *Pohlia*, sporadic occurrences of propagula have been reported. Nyholm (1958) noted that

P. wahlenbergii (Web. & Mohr) Andr. (as *P. albicans*) sometimes reproduces vegetatively "by means of dark reddish gemmae or short branches formed in the leaf-axils." Such deciduous branches have also been observed in North American material of *P. wahlenbergii*.

Amann (1912) described *Pohlia nutans* var. *bulbifera*, saying "Tiges steriles avec des bulbilles axillaires nombreuses ....". However, the type specimen ("Vaud: La Beralla sur Lausanne, 700 m. leg Amann 141.3.14., holotype: Z-Amann !) consists of *Pohlia nutans* (Hedw.) Lindb. with abundant sporophytes in mixture with a few sterile shoots of *P. annotina*. The propagula to which Amann (1912) referred occur on the stems of *P. annotina*. Hegewald (1970) discussed the vegetative reproduction of *P. nutans* by means of "fragile sprouts" (Bruchsprossbildung), and reviewed the nomenclatural history of forms in which such structures occur. Hegewald concluded that "morphologically and anatomically there are no differences between plants of the stat. *gemmiclada* [having Bruchsprossen] and *Pohlia nutans* var. *nutans*." Hegewald (1970) also noted that the stat. *gemmiclada* is only known from Europe, and I have observed neither axillary propagula or "fragile sprouts" in North American material of *P. nutans*.

Lewis and Smith (1978) found that *P. lutescens* (Limpr.) Kindb. occasionally produces flagelliform axillary propagula, but this species is not presently recorded from

North America. *Pohlia baronii* Wijk & Marg. is a propaguliferous species known from Africa, and has propagula very similar to those of *P. annotina*. The plants however, are more highly branched than *P. annotina* and the leaf cells are somewhat more incrassate. *Pohlia baronii* seems to be a distinct species, as noted by Wilczek and Demaret (1974), but as I have not seen sporophytes, I can make no judgement as to its affinities within *Pohlia*. *Pohlia muyldermansii* is a propaguliferous species described by Wilczek and Demaret (1970) as a result of their culture studies on the Pohlias of Belgium. Lewis and Smith (1977, 1978) confirmed the distinctness of *P. muyldermansii* in the British Islands, and described the immature sporophytes (otherwise unknown). From their description, *P. muyldermansii* seems to be phylogenetically related to the propaguliferous Pohlias in the section *Pohliella*, and on the basis of an examination of a number of specimens (*ex* herb Crundwell), I would agree that *P. muyldermansii* is a distinct species. It is not presently known from North America, but I can report *P. muyldermansii* as new to Italy (Artaria, Torno, ± 550 M., 1922 (WTU!)), and Austria (Bauer, Musci Eur. exs. no. 1094, in part, as *P. gracilis* (F!)).

SPECIES CONCEPTS AS THEY APPLY TO THE PROPAGULIFEROUS POHLIAS OF THE SECTION *POHLIELLA*

Henceforth, the phrase, "propaguliferous Pohlias", refers only to species in the section *Pohliella*, and does not include *P. flexuosa*, *P. baronii*, etc. Different assemblages of taxa have different phenetic and phylogenetic relations which must be taken into consideration when erecting a system of classification. Not all taxa being classified at a given taxonomic level are strictly comparable in meaning, and there is no reason why they must be, or can be, as was pointed out by Isoviita (1966), among others. Such individuality with respect to the precise meaning of one species (for example) as opposed to another are implicit in the facts of evolution. It would be surprising, to say the least, if a taxonomist could study a group of species at some arbitrary instant in their evolutionary history, and find each to be separated by a common morphological distance from its closest relative. This would only be possible if all the species being studied had diverged from some common ancestor at the same time, and had continued on their own evolutionary pathways at a constant and identical rate. Such is apparently not the case in most groups. Evolutionary rate is dependent upon a host of factors, including generation time, gene flow, and any factor which affects the rate of genetic recombination (Lewontin 1970). The latter is supposedly regulated by such factors as karyotype morphology, including chromosome number, symmetry and number of cross-over segments (Grant 1958, Stebbins 1958); fecundity (higher number of offspring implies more recombination); relative degree of outbreeding, and effective population size (Grant 1971, Stebbins 1950, Jain 1976a). Obviously, these are factors which differ between species, or even between populations of a single species (Jain 1976b). In addition, most taxonomists are not studying a group of species all of which diverged from one another at the same time, and the consequence is that different species will show different degrees of morphological differentiation from their closest relatives. These differences in evolutionary age and genetic structure lead to an inevitable variability between the precise meaning of what we, as taxonomists, decide to place at the taxonomic level of species.

Within the genus *Pohlia*, there exists many varying degrees of specific differentiation, and consequently, the taxa which we define as species have somewhat varying meanings. While some degree of consistency is, of course, necessary in erecting a classification, I feel that there should also be some degree of flexibility in the definition of a given taxonomic level.

As was suggested in the preceding section, the propaguliferous Pohlias of the section *Pohliella*, form a complex of morphologically similar, presumably monophyletic species. The degree of specific differentiation, in terms of morphology, seems to be somewhat more narrow than in other groups within the genus *Pohlia*. For example, in the section *Pohlia*, *P. elongata* Hedw. and *P. longicolla* (Hedw.) Lindb. are distinguishable on the basis of a combination of both gametophytic and sporophytic features. Likewise, in the section *Mniobryum*, species are characterized and defined by differences in such features as leaf sheen, leaf cell size and shape, exostome color, stomatal morphology, etc. On the other hand, species of the propaguliferous complex are very similar with respect to, and not distinguishable on the basis of, the morphology of their sporophytes. Each of the species share a great number of similarities in both their gametophytes and sporophytes, and differ mainly (though not exclusively) in the morphology and ontogeny of their propagula.

How then do species of the propaguliferous complex compare in meaning to species in other parts of the genus *Pohlia*? If one were to demand absolute consistency in the application of the rank of species within *Pohlia*, then it might be suggested that the propaguliferous taxa be classified at the level of subspecies or varieties. However, I do not think that it is realistic to make such a demand.

Dismier (1905) discussed the taxonomy of *P. annotina* (as *Webera*) and related species, and concluded that some of these taxa would be best considered at a subspecific level. He based this opinion on the observations that the taxa differ exclusively in the morphology of their propagula, and that none of the distinctions are absolute. Similarly, Dixon (1924) felt that the distinctions between taxa are too few (being largely restricted to the propagula), and too variable to be the basis of specific delimitation. Consequently, he placed *P. bulbifera* as a variety of *P. annotina* (as *Webera*) and likewise reduced *W. erecta* (= *P. filum*) to varietal level under the same species. Loeske (1906) gave a comprehensive reply to the arguments of Dismier (1905), saying that he agreed with Dismier that the differences between the propaguliferous species are not absolute, but asserted that the species do differ subtly in gametophytic characters other than those provided by the propagula. He cited pigmentation, size, leaf sheen (gloss) and leaf shape as a few valuable characters which correlate well with differences in propagulum morphology. Loeske (1906) went on to say that he had made a special search for intermediate forms between propaguliferous species, but could report notably few cases of such intergradation. Of all the species which he studied only *P. annotina* and *P. proligera* showed a slight degree of intergradation, and he emphasized that even intergradation between those two species is rare (see Loeske's 1906 paper for a discussion of the differences between forms of *P. annotina* with elongate propagula and *P. proligera;* Loeske 1922 also discussed the lack of intergradation between propaguliferous species).

My own examination of several hundred specimens of the propaguliferous Pohlias has yielded surprisingly few cases in which a plant could not be referred to one or another species with confidence, even in the absence of propagula. There are a few (fewer than five) apparent examples of intergradation between *P. proligera* and *P. annotina*, and slightly more frequent examples between *P. annotina* and *P. camptotrachela*, but between the remaining species, intergrading specimens are practically non existent. In view of this minimal amount of morphological intergradation, I am inclined to treat the propaguliferous taxa at the level of species. Further, each species, as defined by morphological criteria, has been found to be distinct ecologically and phytogeographically, this correlation between morphology and ecology indicating that each taxon so defined possesses considerable biological meaning. Consequently, although species of the propaguliferous complex are somewhat less differentiated from one another in terms of morphology than are species in other sections of *Pohlia*, they seem to be as biologically distinct as any in the genus.

In the absence of breeding experiments and data on the potential for hybridization between propaguliferous species, it is impossible to presently define species by "biological" criteria (e.g. cf. Mayr 1974). Species are presently defined on the basis of morphological criteria, and their biological nature is inferred by the correlation of morphological character complexes with individualistic patterns of ecology and phytogeography. The lack of morphological intergradation, even when growing in interspecific mixtures, is inferential evidence that these morphologically defined species can also be considered biological species.

SYSTEMATIC POSITION OF THE PROPAGULIFEROUS SPECIES WITHIN *POHLIA*

During the time of Dillenius and Linnaeus, the genera *Bryum* and *Mnium* were used in a broad sense to include many of the so-called acrocarpous mosses. Although Dillenius (1741) used a phrase, *Bryum annotinum lanceolatum pellucidum, capsulis oblongis, pendulus*, and Linnaeus (1753) referred to *Mnium annotinum*, neither author seems to have used the name for one of the propaguliferous species (see Schimper 1871, Lindberg 1883, and the section on nomenclatural history of the present work).

Ehrhardt (1779) first used the name *Webera* for a moss, and applied the name to *Webera sessilis* (= *Diphyscium foliosum* (Hedw.) Mohr).

Hedwig (1782), apparently unaware of Ehrhardt's earlier publication, used the name *Webera* for *W. pomiforme, W. hallerianum* and *W. trichodes*. The first two taxa were transferred by Hedwig (1801) to the genus *Bartramia*, while the last, *Webera trichodes*, was later placed in synonomy of *Webera nutans* (Hedwig 1801). Present day *Pohlia* species were placed in Hedwig's (1782) genera *Bryum* and *Mnium*. *Bryum annotinum*, the propaguliferous taxon with which Hedwig was familiar, was placed by Hedwig (1782) with *B. (Leptobryum) pyriforme, B. (Aulicomnium) androgynum* and *B. (Bryum) argenteum*.

Hedwig (1787) first described the genus *Pohlia* with a single species, *P. elongata*. *Bryum annotinum* was retained in the genus *Bryum*. In *Species Muscorum*, Hedwig (1801) distinguished *Mnium*, with acute exostome teeth, cilia and discoid perigonia; *Bryum*, with acute exostome teeth, cilia and "capituliformis" perigonia; *Pohlia*, with acuminate exostome teeth and no cilia; and *Webera*, with acute exostome teeth, cilia, and a monoicous inflorescence. In *Pohlia* he placed only *P. elongata*, in *Bryum*, he included *B. annotinum*, *B. delecatulum* and *B. pulchellum*, among other species presently classified in a variety of genera, and in *Webera*, he referred to *W. nutans*, *W. longicollis* and *W. pyriforme*. He placed the remaining present day *Pohlia* species, *P. cruda*, in the genus *Mnium*. Although Hedwig's (1801) genus, *Webera*, was used by many nineteenth century bryologists for the present genus *Pohlia*, *Webera* Hedw. (1801) is predated by *Webera* Schreb. (1791, Rubiaceae) and *Webera* J.F. Gmel. (1791, Melastomaceae), and is consequently a later homonym.

Following Hedwig's (1801) definition of the genus *Pohlia* by its lack of cilia, Swartz (1799) added *P. inclinata* (= *Bryum stenotrichum* C. Mull., fid. Crum et al 1973), and Bridel (1803) expanded the genus with two more species (*P. intermedia* and *P. pallens*), both of which are presently placed in the genus *Bryum*. Likewise, Hornschuch (1819), using the same generic criteria, described 14 new species of *Pohlia*, most of which are presently considered closely related to, or conspecific with *Pohlia elongata* Hedw. Bridel (1827) and Schwaegrichen (1830) further expanded the genus *Pohlia* by adding species with reduced endostomes, several of which are presently classified in *Bryum*.

Bruch, Schimper and Gümbel (1839) returned to a more inclusive concept of the genus *Bryum*, dividing it into subgroups of undefined rank based mainly on differences in endostome morphology. Their classification recognized four major groups within *Bryum*; *Ptychostomum*, with the endostome and exostome more or less united, lacking cilia; *Cladodium*, with free exostome and endostome, lacking (or rudimentary) cilia, broad leaves and short capsules; *Pohlia*, with free endostome and exostome, no cilia, long, narrow leaves and elongate capsules; and a fourth group possessing cilia, which they further subdivided into *Webera* and *Mniobryum* (cilia not appendiculate) and *Leptobryum* and *Bryum* (cilia appendiculate). Thus, the present day *Pohlia* species were placed in the subgroups *Pohlia*, *Webera* and *Mniobryum* of the genus *Bryum*. *Bryum annotinum*, and *B. ludwigii* var. *gracile*, the two propaguliferous taxa with which they were familiar, were included in the *Webera* group.

Müller (1849) applied a similar, broad definition to the genus *Bryum*, dividing it into *Acidodontium*, *Brachymenium*, *Ptychostomum, Pohlia, Webera* and *Bryum*, based on features of the peristome and inflorescence. The propaguliferous taxa (*B. annotinum* and *B. ludwigii* var. *gracile*), he placed in the *Webera* group, and recognized *Pohlia* by its narrowly perforate endostome segments and rudimentary or absent cilia.

In his *Corallarium*, Schimper (1856) elevated *Webera* to the rank of genus, dividing it into the subgenera *Pohlia* (with *W. acuminata, W. polymorpha, W. elongata* and *W. longicolla*) and *Webera*, including the remaining species having a less reduced endostome.

Lindberg (1865), having discovered Ehrhardt's (1779) application of the genus *Webera* (as divergent from Hedwig's), suggested using *Webera* for the present genus *Diphyscium*, because he did not recognize Hedwig (1801) as the nomenclatural starting point for mosses.

In 1871, Lindberg published (as a *nomen nudum*) the name *Lamprophyllum*, making new combinations for the species which earlier authors (e.g. Bruch et al 1839) had placed in *Webera* and *Pohlia* (as genera, or subgroups within *Bryum*). Lindberg (1871) used the genus *Webera* for *W. sessilis (= Diphyscium foliosum)*. The genus *Lamprophyllum* Lindb. is illegitimate because it included the type species of Hedwig's (1801) genus *Pohlia (P. elongata)*, and was therefore superfluous when published (article 63). Further, *Lamprophyllum* Lindb. is a later homonym of

Lamprophyllum Miers (1854), although Lindberg seems not to have been aware of this fact.

In *Musci Scandinavici*, Lindberg (1879) reduced *Lamprophyllum* to a subgenus of *Pohlia*, dividing the latter into the subgenera *Eupohlia* (sic) and *Lamprophyllum* (still as a *nomen nudum*). This subdivision is essentially the same as that proposed by Schimper (1856, 1876), in which he divided the genus *Webera* into the subgenera *Pohlia* and *Webera (= Lamprophyllum)*. Thus, Lindberg (1879) modified the circumscription of *Lamprophyllum* to exclude the type species of *Pohlia*. Lindberg (1879) further subdivided his subgenus *Lamprophyllum* into the sections *Paroicae, Dioicae,* and *Autoicae*. In 1882, Lindberg described the new species, *P. erecta* Lindb., proposing a new subgenus *Cacodon* (as a *nomen nudum*) to include that species with its erect capsules and reduced endostome.

Limpricht (1892) described *Mniobryum vexans* Limpr. as new to science, erecting the genus *Mniobryum* to accomodate that species plus *Pohlia wahlenbergii* (as *Mniobryum albicans*) and *Pohlia carnea* (as *Mniobryum carneum*). Shortly thereafter, Amann (1893) reduced *Mniobryum* to subgeneric status under *Webera*, within which he included the other subgenera *Pohlia,* and *Euwebera* (sic).

Brotherus (1903), like several European bryologists before him (e.g. Lindberg 1871, Braithwaite 1895), used the generic name *Webera* for the present genus *Diphyscium,* and used *Pohlia* for the bryaceous genus presently under consideration. Brotherus (1903) divided *Pohlia* into the sections *Cacodon*, *Eupohlia* (sic) and *Lamprophyllum*, and described the section *Cacodon* which had been published as a *nomen nudum* by Lindberg (Braithwaite (1895) had validated the name *Lamprophyllum*, also published as a *nomen nudum* by Lindberg). Brotherus (1903) reinstated *Mniobryum* as a proper genus.

Loeske (1910) distinguished two groups of species within the section *Lamprophyllum* Lindb. *ex* Braithw.; the group centered around *P. nutans*, and a second group including the propaguliferous species, which he called section *Pohliella (nomen nudum)*. Jensen (1939) treated the *Pohliella* group as a subgenus, and here provided it with a valid description. Nyholm (1958) followed Loeske in recognizing a section *Pohliella*, and arranged the genus *Pohlia* into four sections; *Mniobryum*, *Pohliella*, *Lamprophyllum* and *Eupohlia* (sic).

A thorough re-evaluation of the subgeneric classification of *Pohlia* is beyond the scope of this work, and should be undertaken in conjunction with a more wide ranging taxonomic revision of at least all the North American species in the genus. For present purposes of discussion, the classification provided by Nyholm (1958) is thought to portray adequately the natural grouping of species within *Pohlia*. The propaguliferous species are included in the section *Pohliella*, which is characterized by its dioicous inflorescence, exothecial cells isodiametric to shortly rectangular with sinuose walls, stomata phaneropore, endostome hyaline, keeled and broadly perforate, and by its well developed but rarely revolvable annulus. Also included in the section *Pohliella* (by Nyholm 1958) are the nonpropaguliferous species *P. erecta* Lindb., *P. lescuriana* (Sull.) Broth., and *P. ludwigii* (Spreng. *ex* Schwaegr.) Broth. Using Nyholm's criteria, the North American *P. cardotii* (Ren. & Card.) Broth. should also be included in this section.

A conspectus of the sections of *Pohlia* is provided below.

1 Annulus absent; capsule often little longer than wide; exostome teeth light to dark brown; endostome hyaline or yellow; exothecial cells isodiametric and often collenchymatous, with sinuose walls; stomata cryptopore or sometimes emergent .... *Mniobryum*

1 Annulus present; capsule considerably longer than wide; exostome teeth yellow to light brown; endostome hyaline; exothecial cells mostly longitudinally elongate and rectangular, with evenly thickened, sinuose or straight walls; stomata phaneropore..... 2

  2 Annulus separating irregularly, rarely revolvable; exothecial cells shortly rectangular

with sinuose walls; plants mostly dioicous .... *Pohliella*

2 Annulus readily revolvable; exothecial cells distinctly longitudinally elongate and rectangular, with straight walls; plants most paroicous or autoicous, sometimes dioicous .. 3

3 Endostome segments narrowly perforate; cilia absent, rudimentary, or occasionally elongate and slightly nodulose; capsule often with the neck as long as, or longer than the urn .... *Pohlia*

3 Endostome segments broadly perforate; cilia long, distinctly nodulose; capsule usually with the neck shorter than the urn .... *Lamprophyllum*

MORPHOLOGY AND LIFE HISTORY

Growth and Reproductive Phenology

Species of the genus *Pohlia* are perennial plants, continuing growth from two to an indefinite number of successive years. The propaguliferous species continue growth by means of renewed apical activity, and basal (sterile shoots) or subfloral (fertile shoots) innovative branching. A single population of *P. proligera* in Alberta has been repeatedly observed over a two and a half year period with the following observations being made. By the end of one year's growing season, most stems in the population are of uniform height, averaging about 1 - (2) cm. high. In the following spring (May or June in Alberta), new, light green shoots arise from within the turf, originating from either fallen propagula of the previous year, or from the perenniating rhizoid system. Renewed apical activity is also evident in some shoots, but growth of young, separate stems occurs at a rapid pace, and accounts for much of the renewed vegetative growth of a given population. It has not been possible to distinguish between the possibilities of new shoots arising from the rhizoid system versus their origin from fallen propagula, and germinating propagula have not been demonstrated for this species in the field. Maximum stem height is reached by mid to late July, and growth is slow or absent for the remainder of the growing season (first frost often occurs in the first week or so of September). Young sporophytes are evident by late June - early July, and are mature and deoperculate by the first of August. Continual observation has not been possible for other propaguliferous species, but in western North America, meiosis in all species is roughly synchronous and occurs in July and August.

Populations of the propaguliferous species are generally limited in size, often occurring in turfs of approximately 100-200 cm^2, often with several such patches growing separately but close together in a given habitat. Large, expansive populations occasionally cover an entire roadbank (for example), but these are the exception rather than the rule. In favorable habitats, *P. filum* sometimes forms an extensive ground cover of many square meters and this species forms large populations more frequently than others.

General Habit

Species of the propaguliferous complex vary in the general habit of their gametophytic shoots from *P. filum* with its slender stems and erect, more or less imbricate leaves at one extreme, to *P. bulbifera* with its short stems and leaves widespread to almost squarrose, at the other extreme. *Pohlia filum* is usually easily recognized in the absence of propagula by its erect leaves. In shaded habitats the leaves are large and appear loosely imbricate while in sunnier situations the leaves are smaller, scarcely overlapping on the stem. *Pohlia bulbifera* is characteristic with its wide-spreading, often yellow-green leaves. *Pohlia proligera* and *P. andrewsii* are similar in general appearance with the leaves erect-spreading and overlapping such that the axillary propagula are not readily observable in the field. The leaves of *P. annotina* and *P. camptotrachela*, on the other hand, are more wide-spreading and distantly spaced, and the axillary propagula are easily observed under a hand lens in the field. *Pohlia tundrae* varies greatly in habit, but in tundra situations, where it is by far most common, the plants form low, compact turfs, and the leaves are erect to slightly spreading. The large propagula (300-600 um long) of this species extend obviously beyond the erect leaves, and make this species readily determinable in the field. In less extreme habitats (e.g. subalpine stream margins or roadbanks), *P. tundrae* grows more loosely and elongate, but the large propagula extending well beyond the leaves are diagnostic. *Pohlia andalusica* is a slender plant with erect to more or less spreading leaves, and characteristically has a cluster of obconic propagula emanating from a single (or two) upper leaf axil(s). *Pohlia drummondii* has wide-spreading leaves (when moist), and the abundant, red, oblong, bulbiform propagula easily distinguish this species. When dry, the leaves are more erect, and are usually strongly carinate.

Like many species of *Pohlia*, the propaguliferous species are quite variable in terms of the degree of elongation of their shoots, this character varying continuously in response to micro-environmental factors. *Pohlia annotina* and *P. proligera* generally grow in protected nooks and crevices of roadbanks, etc., and are rarely found in very exposed, sunny situations. Consequently, these species do not form the very compact, xeromorphous turfs which are sometimes developed in other species. Occasional alpine or subalpine populations of *P. proligera* are more compact in habit, but even in these situations this species does not approach the compact condition sometimes found in *P. tundrae* or *P. drummondii*. *Pohlia annotina* does not occur in tundra situations in North America and therefore does not form equivalent alpine habitat forms. *Pohlia camptotrachela* and *P. annotina* are quite similar in habit and stature when growing in similar habitats. However, *P. camptotrachela* often occurs in more exposed, more gravelly, less humus rich situations than does *P. annotina*, and the more xeric nature of its habitat is sometimes reflected in a more compact growth form as compared to *P. annotina*. *Pohlia andalusica* is one of the most variable propaguliferous species in terms of its growth habit. In exposed habitats the plants are scarcely more than a rosette of small, more or less erect leaves, while in shaded situations the stems may become lax and elongate (to ca. 2 cm. high) with spreading and distant leaves. Judging from the older European herbarium specimens, the names *P. glareola, P. rothii, P. hercynica* and *P. annotina* were often applied to habitat modifications of this species in which the stems were compact (*P. glareola*), intermediate (*P. rothii* or *P. annotina*) or lax and elongate (*P. hercynica*). *Pohlia drummondii* also displays an exceptional plasticity in terms of habit and size. In lowland and montane populations, the plants are generally elongate with more or less spreading, strongly keeled leaves and abundant propagula, while alpine populations are typically compact, with more erect, more concave, less distinctly keeled leaves and few propagula. Intergradation between these extremes appears completely continuous, and alpine plants growing in protected depressions or on the leeward side of windbreaks often approach lowland populations in morphology. *Pohlia andrewsii* is a plant of low to high arctic tundra, and is, accordingly, often compact and dense, like *P. tundrae*. However, plants growing in situations where moisture is abundant and/or the light level low, are often robust and elongate, and can actually be larger than any of the other propaguliferous species. *Pohlia filum* is typically elongate (1-2-[6] cm. high) when sterile, but can occasionally become more compact in exceptionally dry habitats. This species is rather unique among the propaguliferous taxa in that modification in response to moisture stress usually occurs in the size and arrangement of the leaves rather than in the relative elongation of the stem (see above). In *P. filum*, it is generally the size of the leaves, rather than the degree of stem elongation which determines whether the leaves are imbricate or remote. Finally, *P. bulbifera* is rather uniform in stature, typically being less than one centimeter tall, and I have never observed this species forming elongate growth forms much over that height.

Presently, I have not recognized any subspecific taxa based on phenotypical habitat modifications. Some earlier authors have formally named many of the elongate or compact expressions of these *Pohlia* species (as well as most other species in the genus), but these entities should only be considered informally. In particular, Loeske was fond of giving taxonomic recognition to extreme modifications of a variety of *Pohlia* species. He (see Loeske 1909 and Loeske in Bauer 1909) described compact alpine modifications as the variety *carinata*, and referred to lax, elongate forms as the varieties *elata, fila* or *elongata*. It seems that Loeske was well aware that these plants represented nothing more than habitat modifications (standorts - Abänderung, cf. Grebe 1901), but he still felt that they warranted some kind of nomenclatural recognition. For example, he (Loeske 1909) noted that *P. drummondii* (as *P. commutata*), *P. obtusifolia* (as *P. cucullata*), *P. andalusica* (as *P. rothii*) and *P. filum* (as *P. gracilis*) could all form convergent, compact, alpine, carinate forms, and suggested that "Sie können, um die gleichartige Enstehung anzuzeigen, als v. oder f. *carinata* der betrettenden Arten bezeichnet werden" (Loeske 1909, p. 338). Usually, when Loeske was referring to what he apparently considered a habitat form, he prefaced the epithet with an ambiguous designation of rank (e.g. v. oder f. above), a practice which sometimes causes confusing nomenclatural situations (cf. article 35, ICBN). In the case quoted above, the rank of the epithet *carinata* is uncertain, although in other instances (e.g. *P. gracilis* f. *elata* Loeske), Loeske clearly indicated the rank at which he intended the epithet when published (Loeske 1903, p. 221).

Branching Patterns

Branching patterns may prove to be of considerable value in subdividing the genus *Pohlia* into natural assemblages of species. Within the propaguliferous complex, species can be characterized by the mode of branching of 1) sterile shoots, and 2) fertile shoots. Sterile shoots of all the propaguliferous species are usually unbranched, although each does produce a single innovating branch near the base of the stem on occasion. Likewise, with respect to fertile stems (bearing gametangia and/or sporophytes), perichaetial plants are usually unbranched, but the stems may have one or, rarely two, subfloral innovating branches on occasion. Perigonial plants of *P. drummondii*, *P. filum*, *P. andalusica*, *P. bulbifera* and *P. tundrae* branch once (-twice) below the perigonia fairly frequently, while *P. proligera*, *P. annotina* and *P. camptotrachela* very rarely do. I have observed branched perigonial plants in *P. proligera* fewer than five times, and I have never observed them in *P. annotina* or *P. camptotrachela*.

There is some correlation between the mode of branching of fertile plants and the ontogeny of propagula in sterile plants. The tendency (and it is only a tendency, with occasional exceptions) is for species with less reduced propagula (ie. more branch-like, with broadly laminal leaf primordia; see section on propagulum morphology) to have male plants which regularly branch below the perigonia. If the large, more differentiated propagula are considered primitive within the complex (see below), then one might suggest from this correlation that branched perigonial plants are also primitive within the group, and that the reduction in propagulum differentiation has been accompanied by a reduction in branching frequency of perigonial plants. It is of interest that *P. ludwigii*, which Nyholm (1958) considered closely related to the propaguliferous species, has stems that are more highly branched than any of the propaguliferous taxa. It is then possible to speculate that the ancestral propaguliferous

Pohlia evolved from a more highly branched plant, perhaps similar to present day *P. ludwigii*. It may be further envisioned, that evolution occurred via the suppression of axillary branches to form branch-like deciduous propagula (cf. *P. drummondii*), and later, with further reduction, to form the clustered propagula of the more reduced species (see pages 46-57).

Pigmentation

As in many species of mosses, some members of the genus *Pohlia* develop characteristic, though subtle, differences in pigmentation. For example, *P. ludwigii* is usually recognizable on the basis of the pink coloration of its lower, old leaves. Within the propaguliferous complex, differences in pigmentation can be useful in determining problematic specimens. The red coloration characteristic of *P. drummondii* propagula and stems is the most useful field character for recognizing this species. The propagula, when well developed (they are green when very young), take on a cherry-red hue, this feature making the species recognizable without magnification. *Pohlia filum* and *P. drummondii* both have stems which often, but not always, turn nearly black when dry,while stems of the other species remain green, orange or sometimes become red or black at the base, but rarely become black for most of their length. Stems of *P. filum* are green to more or less orange except near the base when fresh, and can usually be distinguished readily in the field from the more red stems of *P. drummondii*. The latter species, in terms of stem color, is more similar in appearance to *Pohlia vexans* (Limpr.) H. Lindb. Since stems and propagula of both *P. filum* and *P. drummondii* often become black when dried, this character-state may be less useful with herbarium specimens; however, many specimens of *P. drummondii* (at least the propagula) quickly regain their red color when moistened. Differences in stem pigmentation in the other propaguliferous species is less pronounced, but propagulum color is often a valuable character. See under the appropriate species for discussions.

Leaf Sheen

Certain members of the genus *Pohlia* are consistently distinguishable by the characteristic sheen of their leaves when dry. Within the section *Pohlia*, *P. elongata* and *P. longicolla* are two similar species which differ noticeably in leaf sheen (among other features). Likewise, in the section *Mniobryum*, *P. vexans*, with its glossy leaves, is easily separated from such related species as *P. wahlenbergii*, *P. carnea* and *P. atropurpurea*, which have dull leaves. From the sporadic occurrence of glossy leaves in widely separated sections of *Pohlia*, it can be suggested that this character state has evolved in the genus more than once.

Within the propaguliferous complex, leaf sheen can be a valuable character with which to distinguish species. *Pohlia proligera*, *P. andrewsii*, *P. tundrae*, *P. bulbifera* and *P. drummondii* have leaves which are consistently glossy when dry. *Pohlia annotina* has leaves which are consistently dull. The leaves of *P. camptotrachela* are almost invariably dull and very similar in appearance to those of *P. annotina*, but a few specimens have been observed with a distinct sheen. Otherwise, the plants are typical (in terms of propagulum morphology) of *P. camptotrachela*. *Pohlia andalusica* often has quite glossy leaves, but some compact, alpine, five-ranked, carinate expressions are rather dull in appearance. Sometimes depauperate plants growing in such habitats as the exposed soil of frost polygons in the mountains of Alaska and the Yukon Territory develop a dull, almost whitish hue. *Pohlia filum* is also somewhat variable in leaf sheen, and even when present, the sheen is not so striking because of the small size and distant arrangement of leaves along the stem.

The reason for the leaf sheen in the propaguliferous species is obscure. The sheen is not at all apparent when the plants are moist, so the effect is probably the result of light reflectance from the dry leaf surface. Because the leaves look glossy only when dry, this character is of little use in distinguishing species in the field. One would expect to find some kind of micro-patterning such as striations or irregular thickenings on the surface of glossy leaves, but no such structural feature has yet been observed. Under the scanning electron microscope, a thin cuticle-like covering was observed on the leaves of *P. proligera*, and it was thought that this could be the cause of glossiness in this species (fig. 11:1). However, this same cuticle-like covering was later observed on the leaves of *P. annotina* and other nonglossy species, as well as on the propagula of some species. Whatever the structural cause of the leaf sheen is, its intensity is more or less subject to variation in response to micro-environmental factors. In any species which normally has glossy leaves, this character state is best developed in shaded situations (perhaps opposite what one might logically expect). This is most clearly exemplified by *P. andalusica*. When growing in moist, shaded roadside ditches or other protected habitats, the leaves are normally extremely glossy, as well as being more or less spreading when moist and somewhat flexuose when dry. At the opposite extreme, populations of *P. andalusica* growing in exposed tundra habitats, frost polygons, etc., have leaves which are dull, and the leaves are more erect and stiff in appearance. Populations growing in unusually moist, though exposed and sunny situations in alpine tundra, generally have leaves with a distinct sheen, indicating that moisture rather than solar radiation is probably the determining factor in control of leaf sheen in this species. *Pohlia tundrae* also varies somewhat in leaf sheen, and the occasional populations found below treeline in shaded habitats have more glossy leaves than their alpine counterparts. Unlike *P. andalusica*; however, alpine populations of *P. tundrae* do not take on the dull, pale appearance which such populations of the former species sometimes display.

Leaves

The leaves of most *Pohlia* species vary greatly on a single stem, becoming larger and longer from the small, first formed, "immature" leaves near the base, to the full sized leaves just below the stem apex. In most species the mature leaves (those fully developed leaves just below the stem apex) are narrowly to broadly lanceolate, although in some species they may be described as ovate-lanceolate (e.g. *P. ludwigii* fig. 1:9). Leaves of sterile shoots have plane to slightly reflexed margins (except *P. crudoides* and *P. cardotii*), and are commonly toothed near the apex or occasionally almost to the base. The propaguliferous species have narrowly to broadly lanceolate leaves (e.g. fig. 1:7, 8), these being rather variable both within and among species, and are consequently of little value in discriminating between species.

Leaf size is sensitive to environmental factors, and varies as much within species as between them. The degree of decurrency of the leaves is also variable, this character correlating closely with the degree of elongation of the stems. Shoots in which the stems are elongate have decurrent leaf bases while compact shoots with short stems tend to have non-decurrent leaf bases. The leaf bases of *P. ludwigii* are consistently more decurrent than those of any of the propaguliferous species.

The leaves subtending the female inflorescence are gradually differentiated as lanceolate to linear-lanceolate perichaetial bracts (fig. 1: 1-6), and commonly have the margins recurved from just above the base to just below the apex. The bases of these perichaetial bracts are non-decurrent.

Leaf Cells

The upper median leaf cells of all *Pohlia* species are smooth and vary from shortly rhombic (*P. cardotii*) to elongate or linear-hexagonal. In some species, such as *P. nutans* and *P. elongata*, the cell walls are strongly incrassate, but in most, including the propaguliferous taxa, they are thin-walled. The propaguliferous species all have elongate-hexagonal to linear-hexagonal upper cells (fig. 1: 10), and more or less elongate-rectangular basal cells (fig. 1: 11). As there is a great deal of variation within a single leaf, and among leaves from a single population, leaf cell shape is of limited value in identifying species of the propaguliferous complex. However, the following tendencies are worthy of note. Of *P. drummondii* and *P. filum*, the latter species generally has shorter, slightly broader cells. Leaf cell length-width ratio seems to be correlated with leaf length-width ratio, however, so forms of *P. filum* (growing in moist habitats) with large, well developed leaves have cells which completely overlap in shape with those of *P. drummondii*. Of *P. annotina* and *P. proligera*, the former tends to have shorter, broader, less frequently vermicular cells, but considerable overlap does occur, as with *P. filum* and *P. drummondii*. *Pohlia andrewsii* also tends to have somewhat shorter, broader cells than does *P. proligera*, to which it is similar in its medium to robust stature and glossy leaves, but again the distinction is obscured by considerable overlap. Some collectors have confused sterile turfs of *P. elongata* or *P. nutans* with *P. drummondii*, but the former species are readily distinguished by their incrassate cell walls and dull, often stiff looking leaves. The cells of the perichaetial bracts of *P. annotina* are sometimes slightly more incrassate than those of leaves on sterile plants, but do not approach those of *P. nutans* or *P. elongata*.

Costae

Members of the Bryaceae have single, well-developed costae, extending to mid-leaf or beyond. Unlike many species of *Bryum*, the costa of most *Pohlia* species ends 2-6 cells before the leaf apex (the European *P. marchica*, is reported to have the costa sometimes shortly excurrent, Nyholm 1958). Among the propaguliferous species, *P. drummondii* and *P. filum* tend to have shorter costae, ending 4-6 cells below the apex, than do the species with clustered propagula, which have the costa ending within 2-3cells of the apex. However, this is of little practical value in determining specimens.

The anatomy of the costa in transverse section is uniform within the propaguliferous complex, and seems to be so throughout the genus *Pohlia*. The costae of leaves on vegetative shoots appear rounded adaxially (ventral) and strongly convex abaxially (dorsal) (fig. 2: 3). Near the base of the leaf, the costa has two to four well marked guide cells extending from lamina to lamina, and a greater or lesser development of thick-walled stereid cells abaxial to the guide cells. There may also be a few stereids on the adaxial side of the guide cells. Along the adaxial surfaces of the costa, the cells are typically larger than the adjacent stereids, but not so large as the central guide cells (fig. 2: 3). The guide cells extend well up toward the leaf apex, gradually becoming less distinct and finally disappearing in the upper third of the leaf (fig. 2: 1-3). The cells of the lamina are somewhat irregular in shape, and a few often bulge adaxially or abaxially. The bulging shape results from the cell itself, and is not because of a thickened cell wall (fig. 2: 3). The costae of perichaetial bracts are more strongly developed than those of sterile plant leaves (fig. 2: 4). In shape, they are broader and less rounded- convex abaxially, and the stereid cells are considerably more developed.

Stem

Like the costa, the stem in transverse section appears to be uniform throughout the propaguliferous complex (fig. 2: 5, 6). It appears roughly pentagonal in shape, averaging about 0.3 mm. in diameter near the base, gradually diminishing in size toward the apex (fig. 2: 6). In general anatomical plan, the stem is similar to the seta (see below), consisting of a rather abruptly differentiated central strand of small, hyaline, thin-walled cells (often collapsed), surrounded by larger, hyaline, slightly thicker-walled cells. These in turn grade into 2-4-(6) layers of thick-walled, pigmented cells. In *P. drummondii*, these latter cells are red, in the other species they are more often orange or pink (cf. above). The cells around the periphery of the stem are smaller, and very thick-walled.

In the angles of well developed, pentagonal stems, there often exists groups of small, notably thick-walled cells.

Perigonial Bracts

The morphology of the perigonial plants differs between propaguliferous species, and these can sometimes be of great value in determining difficult specimens, especially when the plants are fertile and propagula are scarce. Each species has terminal, bulbiform perigonia on either unbranched stems, or the stems may be branched once, or rarely twice, below the inflorescence (see previous section on branching). The perigonia are surrounded by a few leaves which are larger, but otherwise similar in shape to the lower stem leaves (fig. 3: 1) and internal to these occurs a series of gradually differentiated perigonial bracts (fig. 3: 2-6). The outer bracts (fig. 3: 3) are more or less narrowly acuminate from an ovate-concave base, and these grade into the inner bracts which have the broad base, but lack the elongate acumen (fig. 3: 5, 6). When discussing species-specific morphology of the perigonia, it is most useful to compare the outer bracts (e.g. fig. 3: 3) as a standard of reference, as all the species have broadly concave, acute, inner bracts (fig. 3: 5, 6).

When Hagen (1899) published the name *Webera torrentium (= P. filum)*, he briefly discussed the morphology of the perigonial plants and suggested that the shape of the perigonial bracts is useful in distinguishing *P. drummondii* from *P. filum* (as *W. torrentium*). According to Hagen (1899, p. 112), the perigonial bracts of *P. filum* are abruptly narrowed to a short, triangular acumen from a broad, strongly concave base, while the bracts of *P. drummondii* are longer and linear-lanceolate from a similar concave base. While *P. filum* does have outer bracts which are consistently shortly acute from the ovate-concave base (fig. 4: 11), *P. drummondii* is variable in this respect, and can sometimes have bracts which are almost as short as those of *P. filum* (fig. 4: 10). In general, the overall laxness of a plant of any of the propaguliferous species is shown in the length-width ratios of its leaves, leaf cells, sometimes propagula, and also the perigonial bracts. That is, a population of *P. drummondii* growing in a shaded habitat will have relatively long leaves, leaf cells and also perigonial bracts. Plants of *P. drummondii* growing in exposed alpine tundra generally have short stems, broad leaves, short cells, and short, abruptly acute perigonial bracts like those of *P. filum* (fig. 4: 10). Given such overlap in perigonial bract morphology, my observations agree with those of Hagen that male plants of *P. filum* and *P. drummondii* are often useful in distinguishing these species.

Most other propaguliferous *Pohlia* species have outer perigonial bracts which vary from shortly acute to longly acuminate. These include *P. andrewsii, P. tundrae, P. proligera* and *P. andalusica* (fig. 4). In each case, the general laxness of the plants is correlated with the degree of elongation of the perigonial bracts. The most typical condition, resulting from the most frequently encountered ecological situation in these species, is to have bracts which are shortly acuminate (fig. 4: 2-5, 12), and that the less frequent narrowly and longly acuminate bracts reflect an unusually shaded habitat (fig. 4: 1, 6, 13). *Pohlia annotina* and *P. camptotrachela* both consistently have outer bracts which are narrowly acuminate from an ovate, concave base (fig. 4: 7, 8). I have never observed short (outer) bracts on either species even though *P. camptotrachela* sometimes occurs in exposed, sunny habitats. It is probable that in these cases bract morphology is more rigidly fixed and less plastic than in the other species. The long acuminate bracts of *P. annotina* make the perigonial plants very conspicuous, and led H. Lindberg (1900) to propose the name *P. grandiflora* for plants with this character state. The perigonial plants of *P. bulbifera* are quite different from those of the other propaguliferous species. The outer bracts are more widespreading than in the other species, and so the perigonia tend to appear discoid, rather than truly bulbiform. In gross form, they resemble perigonia of species in the section *Mniobryum*, although they are considerably larger.

Pohlia cruda, when dioicous, also has perigonial plants which have the outer bracts more or less wide-spreading.

Propagula

Propagula have long been recognized as occurring in some species of *Pohlia*, with early authors recognizing only one propaguliferous species (e.g. Leers 1775, Hedwig 1801). Correns (1899) was the first bryologist to culture living propaguliferous Pohlias, and recognized six species on the basis of differences in ontogeny of the propagula. More recently, Wilczek and Demaret (1970, 1974) and Lewis (1976) have confirmed the species-specific nature of propagulum morphology in European members of this complex by means of culture studies. Taxonomic and nomenclatural confusion has arisen because of inadequate descriptions of these taxa, and too often descriptions have confused the manner in which propagula arise, with the manner in which they may appear at certain times of the year. In some species (e.g. *P. annotina, P. andalusica*), propagula continue developing while they are attached to the stem, while in others (e.g. *P. filum, P. proligera*), they change little after their initiation (see below). While it is useful, and in fact essential, to describe the various ways in which propagula appear and change through time, the propaguliferous species can best be defined by the origin and distinct pathways in which their propagula develop. Several species have continually been confused, because although they have propagula which arise in different manners, these propagula may converge in many features at various stages of development. To cite one example, the propagula of *P. andalusica* arise in clusters in each leaf axil, and when young, appear obconic with the leaf primordia conspicuous, but restricted to the apical region (fig. 5: 1, 2, 5). However, specimens collected later in a growing season sometimes have only a single, larger propagulum, or two or three, scattered in one to several leaf axils (lower leaves, fig. 5: 5). Upon collecting such a plant, it is possible to describe *P. andalusica* as having the propagula borne singly in each leaf axil. In fact, they had actually arisen in clusters, with most of the smaller propagula having already fallen from the stem. *Pohlia filum*, in contrast, has propagula which actually do arise singly in each leaf axil, and even when young, these appear rounded-bulbiform with several apical leaf primordia (fig. 5: 6-9). While a comparison of young shoots of *P. andalusica* and *P. filum* presents no problem in distinguishing the two species, an older shoot of *P. andalusica* may appear very similar to *P. filum* because of its single, bulbiform propagula. This kind of developmental convergence, however, is not to be confused with actual intergradation between the two species, with its implication of genetic interchange.

All species presently recognized as distinct have been grown in controlled environment facilities, and an attempt was made to formally define each on the basis of the species-specific developmental pathway which characterizes its propagula.

Propagula of species in the section *Pohliella* may arise in one of two ways. In *P. drummondii* and *P. filum*, they arise singly in each leaf axil (rarely two per axil), while in the remaining species they invariably arise in clusters of six or more. In basic ground plan , propagula of all species are similar. They consist of a more or less differentiated propagulum body, and one to five or six peglike (e.g. fig. 6: 2) or laminal (e.g. fig. 7: 9) leaf primordia arranged in a spiral near the propagulum apex (fig. 11: 2,3). Variation between species occurs in the degree of differentiation of the propagulum body, and in the mode of origin and subsequent development of the leaf primordia. Species also differ in the degree of translucency of their propagula, but such differences are not absolute and are of less discriminative value than the differences in ontogeny (translucent propagula are illustrated showing the external cellular outlines while the more opaque propagula are shaded).

The propagulum body consists of a mass of thin-walled cells which vary in shape from isodiametric (fig. 6: 9-11, 20) to elongate-rectangular (fig. 6: 18) or almost linear-vermicular (fig. 6: 5). This degree of cellular elongation often determines the overall shape of the propagulum. In some species (e.g. *P. proligera* fig. 6: 13-18), the body cells are little affected by the environment, appearing consistently elongate; in other species (e.g. *P. camptotrachela* fig. 6: 9-12), they are equally uniform, but isodiametric to shortly rectangular; while in still others (e.g. *P. annotina* fig. 6: 1-8), they are quite variable, appearing isodiametric in some populations (fig. 6: 3) and linear-rectangular in others (fig. 6: 6).

Propagula of all species arise on a uni- or multicellular stalk, the latter types sometimes being as much as four cells in diameter. The stalk in some species consistently remains attached to the stem and is not usually observed. In *P. proligera* and *P. annotina*, the propagulum base is gradually narrowed to the stalk (fig. 6: 3, 15), while in others it is abruptly differentiated (e.g. *P. filum* fig. 7: 15, *P. camptotrachela* fig. 6: 11). Growth of propagula which arise singly (i.e. those of *P. drummondii* and *P. filum*) begins with the elongation and transverse division of a group of superficial stem cells giving rise to a multicellular, multiseriate stalk (fig. 7: 15). Later, an apical cell with three cutting faces is differentiated and subsequent development of the propagulum occurs by division of this apical cell (Correns 1899). Clustered propagula likewise arise via the elongation and transverse division of superficial, axillary stem cells. In species with clustered propagula, a larger number of axillary cells elongate, and instead of forming a multiseriate stalk like those of the single propagula, they give rise to many, separate propagula (fig. 6: 23). Some of the elongating stalk cells divide at an oblique angle (to the direction of elongation), such that two or three propagula may arise from a common stalk (fig. 6: 23). Subsequent development of clustered propagula occurs through the division of an apical cell with two or three cutting faces (Correns 1899).

The origin and development of the leaf primordia can likewise proceed in several directions. In some species (*P. drummondii, P. filum, P. andalusica* and *P. bulbifera*), the leaf primordial initials at the apex of the propagulum body elongate only slightly, and begin dividing on a single plane to produce a laminal, ie. leaf-like leaf primordium (fig. 7 shows examples of propagula in which the leaf primordia are laminal in origin). In other species (*P. proligera, P. annotina*), the leaf primordial initials elongate, but subsequent divisions producing a laminal appendage are delayed for some time (*P. annotina*) or rarely occur to any extent (*P. proligera*). The result of this pattern of development is a fingerlike, ie. peglike, leaf primordium (fig. 6 shows propagula having peglike leaf primordia). In *P. tundrae*, the leaf primordial initials elongate as in the former two species, but very shortly thereafter they divide, producing a laminal leaf primordium (fig. 7: 1, 2). The division of the primordium cells occurs soon enough after elongation, that by the time the propagula are large enough to be observed under a dissecting microscope, they have conspicuously laminal primordia. The leaf primordia of *P. camptotrachela* do not divide producing a laminal appendage, nor do they greatly elongate like those of *P. proligera* or *P. annotina*, and the result is an apical group of short, peglike primordia (fig. 6: 9-12). The origin of the leaf primordia in *P. andrewsii* exemplifies yet another variation on this ontogenetic theme. The primordial initials at first elongate only slightly (cf. *P. camptotrachela*), and the propagula of *P. andrewsii* often appear with two to five short, peglike, incurved primordia (fig. 6: 19, 21). Subsequently, however, the peglike leaf primordia of this species undergo a series of anticlinal divisions such that a laminal, though inconspicuous and still incurved, leaf primordium is formed (fig. 6: 20). Typically, a given stem of *P. andrewsii* has a mixture of propagula present, some in which the primordia have become laminal, and others in which the primordia are still peglike.

It can thus be seen that 1) propagula of each species develop according to a general ground plan common to all the propaguliferous species and 2) it is possible to arrange the species along a continual morphological gradient from those of *P. drummondii* (most complex) at one end, to those of *P. proligera* or *P. camptotrachela* (least complex) at the other end. Furthermore, it has been argued (see introduction) that based on the morphological uniformity of sporophytes among the propaguliferous species, this complex probably forms a monophyletic assemblage. The question then, is in which direction should this morphological gradient be interpreted; ie. did the complex propagula become reduced through the course of evolution to form the simpler types, or did the evolutionary history of this group occur in the opposite direction, from simple to complex.

Even the pre-Darwinian taxonomists who studied this group (e.g. Hedwig 1801, Bruch et al 1839) compared the propagula, both in position and in form, to poorly developed branch buds, and implicitly considered them morphologically analogous (if not homologous) with such buds. Correns (1899) studied the group intensively, and concluded that the propagula are homologous with axillary branches. He proposed (1899 p. 158) a phylogenetic scheme in which *P. drummondii* was considered primitive and *P. proligera* was considered the end product in a reduction series. His interpretation was based on the following considerations. 1) The axillary origin of the propagula is comparable to the axillary origin of branches in this genus. 2) Propagula of each species develop according to a pattern common to all species in the group. 3) Each propagulum grows by division of an apical cell similar to that by which branches develop. 4) Branches have groups of rhizoid initials in the axils of their leaves, and these rhizoid initials are preserved in a spiral arrangement on the propagula even where the subtending leaves have been reduced, or lost altogether.

Since the morphological gradient interconnecting all the propaguliferous species exists, and since evolution must have occurred in one direction or the other (assuming the group is monophyletic), I feel that Correns' (1899) arguments are both logical and convincing. The propagula of *P. drummondii* are so branch-like in form, it is almost an arbitrary decision to call them propagula rather than deciduous branches. When grown in culture (fig. 6: 22), the propagula of *P. drummondii* often elongate greatly, taking the form of typical axillary branches with well defined stem and costate leaves (Smith and Whitehouse 1978, reported similar phenomena in field-collected populations of the propaguliferous species, *Bryum bicolor* Dicks.). The only difference between propagula of *P. drummondii* and true branches is that the propagula are borne on a multicellular stalk rather than being directly confluent with the stem. Ontogenetically, the difference is a relatively simple one. If the superficial stem cells immediately form an apical cell dividing along three planes, the result is an axillary branch. In the case of *P. drummondii*, the formation of an apical cell is delayed, and is preceded by the elongation and transverse division of the cells which form the stalk, and which also allow the propagulum to be readily deciduous. It should be pointed out however, that although the propagula are probably homologous to branches, this does not necessarily prove that a "proto-propaguliferous" *Pohlia* actually had well developed axillary branches which gradually became reduced through the course of evolution. It is possible that only the axillary branch initial was present in an ancestor, and that this group of species evolved by the production of only partially developed "branches", while other species (e.g. *P. ludwigii*) produced true axillary branches. However, this possibility is a less likely explanation for the almost continuous gradient of propagulum complexity present in this group, since if the immediate ancestor had only the axillary branch initial, then simple types of propagula could be primitive, or intermediate types, etc., and evolution need not have occurred in one direction or the other.

Beyond the interpretation that evolution has occurred in the direction from complex propagula to simple propagula, it would be highly speculative at present to place all the species in a linear or dendritic phylogenetic arrangement. It is more likely that reduction has occurred along several parallel lines simultaneously, and consequently it is only possible to speak of progressively advanced *levels* of evolution. From the *P. drummondii* level of evolution, *P. filum* propagula could have evolved by the simple reduction in number and size of its leaf primordia. Ecologically, *P. filum* often occurs in more xeric habitats than *P. drummondii*, and its more slender stems, more erect leaves, and propagula with fewer, smaller leaf primordia could be considered adaptive for this ecological shift. When growing in moist habitats such as shaded riverbanks (or enclosed culture dishes), *P. filum* often has larger, more spreading leaves and the propagula have considerably larger, more flexuose leaf primordia. The propagula of *P. andalusica* are similar to those of *P. drummondii*, and their clustered origin is the result of relatively minor differences in their early ontogeny (see above). Correns (1899) felt that the difference between the clustered versus single origin of propagula in these species did not even warrant taxonomic distinction (see pages 99-100). *Pohlia tundrae* propagula are similar to both *P. andalusica* and *P. drummondii*, differing from the former in being produced in more numerous leaf axils on each stem and having the body cells more elongate (producing a cylindrical propagulum), and from the latter in arising in clusters. Again, these are probably relatively simple developmental differences. *Pohlia bulbifera* propagula are very similar to those of *P. andalusica*, differing in the more globose body and in having the primordia in a tight spiral, almost whorled. There is an apparent discontinuity in the mode of leaf primordium development between those former species which have the leaf primordia arising as laminal appendages, and the following species whose leaf primordia are represented only by peglike outgrowths, but this developmental difference is bridged by *P. andrewsii*. The primordia of *P. andrewsii* begin as short, poorly formed peglike projections, but after a short delay they undergo repeated divisions to produce truly laminal appendages. In fact, *P. annotina* also bridges this gap, in that the leaf primordia on old propagula (fig. 6: 7, 8) do eventually begin to divide, producing laminal appendages which had arisen as peglike outgrowths. This greater delay in leaf primordium differentiation can be interpreted as indicative of a slightly more advanced level of propagulum evolution in *P. annotina* as compared to *P. andrewsii*. *Pohlia camptotrachela* is indistinguishable from *P. annotina* in all morphological respects except in its propagula, and the two are probably closely related. The former species often occurs in more xeric habitats than *P. annotina*, and this ecological difference may explain the smaller, more globose propagula (with less surface area), and the poorly developed, short, often incurved leaf primordia. *Pohlia proligera* propagula are not unlike young *P. annotina* propagula, but produce only a single or two, elongate peglike leaf primordia, and do not continue growth while attached to the stem as do those of *P. annotina*. It is probably not so closely related to *P. annotina* as is *P. camptotrachela*, as indicated by differences in other gametophytic features such as size and leaf sheen.

It can be seen that the different forms of propagula in this group develop according to a common ground plan, and that the propagula of each species could have arisen by progressive ontogenetic modification taking the form of small reductions in the differentiation of the propagulum body, and in variations in the origin and subsequent development of their leaf primordia (fig. 8).

Setae

Setae of the propaguliferous species are erect, but abruptly bent at the point of attachment to the capsule such that the latter is positioned at 90°-180° from the vertical. Within these limits, capsule position is variable both within species and between them (fig. 3: 9-11). In transverse section, the setae are about 0.20 to 0.25 mm. in diameter and are anatomically similar to the stem. In the central portion is a cylinder of thin-walled cells more or less abruptly differentiated from the larger, thicker-walled cells surrounding them. The periphery of the seta is occupied by 3-5 layers of small, thick-walled cells (fig. 3: 7, 8). No anatomical variation of taxonomic value has been observed, although the setae of each species may vary as much as 0.5 mm. in diameter.

Exothecial Cells

Exothecial cell shape provides an important criterion on which to base infra-generic classification within the genus *Pohlia*; see Nyholm 1958. The propaguliferous species show little or no inter-specific variation in this character which is uniform throughout the section *Pohliella*. Exothecial cells of the urn are more or less rectangular to isodiametric, and have evenly thickened, strongly sinuose walls (fig. 10: 2). Near the rim they are more or less abruptly smaller, less sinuose-walled, more regularly isodiametric and occasionally somewhat collenchymatous (fig. 10: 3). At the point of attachment of urn and seta, the exothecial cells grade into the long, narrow superficial cells of the latter, gradually appearing less sinuose-walled (fig. 10: 1).

Stomata

Stomata of species in the section *Mniobryum* are immersed or sometimes immergent, while those of species in the sections *Pohlia, Lamprophyllum* and *Pohliella* are superficial. Stomata of the propaguliferous species are numerous in the neck of the capsule, and are generally 32-55 um long. No interspecific differences in stomatal morphology have been observed, and stomata on a single capsule of any of these propaguliferous *Pohlia* species may exhibit the full range of size exhibited by the complex (e.g. *P. tundrae*, fig. 9: 8-10).

Annuli

The sections *Pohliella, Pohlia* and *Lamprophyllum* have well developed annuli while the remaining section *Mniobryum* lacks them altogether. In *Lamprophyllum* and *Pohlia,* the annuli are readily revolvable, but in the section *Pohliella* the annuli generally remain attached to the urn or the operculum, rarely (though occasionally) being revolvable. The observation of Muller (1862a, 1862b) that his new species *B. drummondii* lacked an annulus was in error (Demaret and Wilczek 1978). The propaguliferous species have annuli consisting of 2- (3) rows of cells, the number being somewhat variable around the circumference of a single capsule (fig. 9: 1-6). The upper row (adjacent to the operculum) usually consists of slightly larger cells (ca. 60 um long, 35 um wide) than the lower row (ca. 35 um long, 35 um wide).

Nyholm (1958) described the annuli of *P. drummondii* as consisting "of 1- (2) rows of large, separating cells", and illustrated an annulus with only a single cell row (fasc. 3, p. 200). Likewise, under *P. annotina*, Nyholm (1958 p. 202) described the annuli as consisting "of a single row of large cells". It is puzzling that there should be this discrepancy in our observations on the annuli of these *Pohlia* species, especially since I find the annuli to be uniform both within species and between them. Perhaps there is this difference between North American and Fennoscandian populations, but otherwise I find that specimens from the two continents agree in every respect.

Opercula

Opercula of all propaguliferous species are conic and often apiculate, rarely appearing somewhat umbonate (fig. 9: 16-19). They do not, however, approach the umbonate condition which is very characteristic of opercula in *P. obtusifolia* (fig. 9: 14, 15).

Calyptrae

No systematic study was made of calyptrae because they are scarce and difficult to find in herbarium specimens. From field observations they are smooth and cucullate, and appear to be uniform throughout the complex.

Exostome

The peristome of species in the propaguliferous complex is diplolepideous and double, being described as the so-called Bryoid type (fig. 9: 7). The exostome teeth are lanceolate and gradually acute (fig. 10: 5-7). They average about 230 um in length, but vary as much as 50 um in length on a single capsule. Between capsule variation in exostome tooth length is as much as 120 um, but no consistent differences could be found between species. Margadant and Meijer (1950) discussed even greater variation in exostome length in the genus *Orthodontium* Schwaegr.

On the dorsal surface the exostome teeth are coarsely papillose in the upper third, gradually becoming more finely roughened toward the base (fig. 10: 5). The dorsal commissure is not conspicuous, but is readily visible under a compound microscope. On the ventral surface the teeth are coarsely papillose to a lower level than on the dorsal surface, and large papillae cover the ventral lamellae all the way to the base of the tooth (fig. 10: 6). In the areas between lamellae on the ventral surface, coarse papillae extend about half way to the base of the tooth. The lamellae are well developed and conspicuous, as can be seen in lateral view of an exostome tooth (fig. 10: 7). The teeth are margined, though not conspicuously, with the dorsal plates wider, although the ventral plates are thicker (fig. 9: 11-13). In color, the exostome teeth vary from yellow to light- or occasionally dark-brown, usually darkest near the base.

Endostome

The endostome consists of a hyaline, finely papillose basal membrane from whence 16, hyaline, keeled, broadly perforate segments arise alternating with (0)- 1-3, more or less developed, usually nodulose cilia (fig. 10: 4). The basal membrane extends almost one half the height of the exostome teeth, and is finely papillose, as are the lower portions of both segments and cilia. The upper portions of the segments and cilia are more coarsely papillose adjacent to where the exostome teeth also become more coarsely papillose (on the dorsal surface) (fig. 10: 4, 5).

Spores

Spores of the propaguliferous species are round, apolar, and are (13)- 17-26- (35) um in diameter. No consistent differences could be found between species in terms of spore size, but under the scanning electron microscope, spores were found to differ between species in external ornamentation. Terminology for external ornamentation follows the classification of Faegri and Iversen (1975) for pollen grains.

Spores of the propaguliferous species vary from clavate to baculate. Spores of *P. drummondii, P. tundrae, P. bulbifera, P. andrewsii* and *P. camptotrachela* have sculpture elements which are taller than broad, and which widen distally from a narrowed base (clavate) (fig. 12: 4), 13: 1-3, 4). *Pohlia annotina* and *P. proligera* (fig. 13: 4, 6) have sculpture elements which are little, if at all, taller than broad, and which do not, or rarely, broaden distally from a narrowed base (baculate). *Pohlia filum* and *P. andalusica* (fig. 12: 5, 6) have tall sculpture elements in relation to their width, but they broaden distally only slightly. It should be added that spores from two capsules of each species were observed under the SEM, but although differences shown here appear to be consistent, no extensive study was conducted on the morphological variation between spores of one species.

NOMENCLATURAL HISTORY OF THE PROPAGULIFEROUS TAXA

The occurrence of asexual propagula in the leaf axils of certain *Pohlia* species had been noted since the time of Leers (1775), Roth (1794), and Hedwig (1782, 1801). Until well into the nineteenth century, however, only one propaguliferous *Pohlia* was recognized at the species level (as *Mnium* or *Bryum annotinum*) and this epithet was used as a catch-all for any *Pohlia* specimens bearing axillary propagula. According to Bridel (1803), there was considerable early confusion surrounding the name *Bryum (Mnium) annotinum*, this being largely the result of some authors incorrectly interpreting sterile and fertile expressions of the species as distinct taxa (Bridel 1803 pp. 33-34). For example, A.G. Roth described *Trentepohlia erecta* as a new taxon in 1794, but by 1800, he had changed his mind and reported that his plants were nothing more than sterile propaguliferous forms of *Bryum annotinum* (Roth 1794, 1800). In his discussion of *Bryum annotinum*, Bridel (1803) provided an interesting insight into the human side of Johann Hedwig, who was apparently rather critical of those bryologists who had erroneously considered sterile and fertile forms of *Bryum annotinum* to be distinct species. Thus, Bridel quoted Hedwig's irritation, "*vt eo evidentius sestinantioris observationis, ae praeposteri decreti circa naturale producta damnum eluceat*"

(Bridel 1803 p. 34).

Authors of the mid eighteenth century (e.g. Dillenius 1741, Linnaeus 1753) used the name *Bryum (Mnium) annotinum* without reference to propagula, and most likely used the name for taxa quite unrelated to that which it is presently applied. When propagula were first used in the specific diagnosis of the species (Leers 1775, Hedwig 1801), only the presence of these propagula were considered diagnostic, and no attempt was made to distinguish species based on differences in number, size or morphology of the propagula. Probably only with the development of more accurate means of magnification, in conjunction with continued field experience, were segregate taxa gradually recognized and nomenclaturally distinguished from *Bryum annotinum* Hedw. As new taxa were described, a great deal of nomenclatural confusion enveloped the propaguliferous Pohlias as a result of the fact that various authors applied the same epithet to different species, depending upon which species happened to be most common in their own geographic region. This problem has been exasperated by a lack of accurate illustrations and detailed morphological descriptions accompanying original diagnoses and subsequent new combinations for the propaguliferous species in *Pohlia*.

The nomenclature of *Bryum annotinum* Hedw. has been extensively discussed in the twentieth century, notably by Correns (1899), Loeske (1905-1922), Warnstorf (1904) and

Buch (1906) and more recently by Koch (1951), Margadant (1968), and Lewis and Smith (1978), among others. The nomenclatural and taxonomic history of *B. annotinum* Hedw. is not unique in botanical investigations, and our knowledge has progressed gradually with the increased insight and understanding gained from continuing studies, and by the passage of time. In this respect, I cannot agree with the comment by Lewis and Smith (1978) that many earlier discussions (of the nomenclature of *B. annotinum*) were put forward "without any useful conclusions being arrived at".

The present nomenclatural study was undertaken as part of a taxonomic revision of the propaguliferous species of *Pohlia* in North America, and detailed morphologic and taxonomic discussions will be found in a later section. The present discussion is intended as a nomenclatural history of the propaguliferous complex, and it is acknowledged that many taxonomic details are omitted for brevity (but included in a later section under the appropriate species), while other literature of only indirect nomenclatural relevance is reviewed here in some detail (e.g. pre-1801 references). It is hoped that this historical survey of the literature will enable the reader to adequately judge the merits of the nomenclatural conclusions arrived at in the present study. As a result of an extensive literature survey and examination of type specimens, the nomenclatural citations given in Table 1 are considered the earliest valid combinations for the North American propaguliferous Pohlias.

The present discussion is organized into the following sections.

- Developmental variation as a source of nomenclatural confusion
- Historical survey of the literature
    - The Dillenian era
    - The Hedwigian era
    - The Loeskean era
- Review of recent nomenclatural arguments
- Present nomenclatural conclusions
- Suggestions for lectotypification

Developmental variation as a Source of Nomenclatural Confusion

In general, bryologists have distinguished two groups of propaguliferous species in the past; those with solitary, bulbiform propagula (e.g. *P. drummondii* and *P. filum*) and those with smaller, clustered propagula (e.g. *P. annotina* and *P. proligera*). However, as early as the beginning of this century, Correns (1899), Warnstorf (1900) and Loeske (1906) observed that some species could have either or both types of propagula at various times of the year. (In fact, Bruch, Schimper & Gumbel (1839) compared the propagula of *B. annotinum* to young branches and thus implicitly considered developmental variation of the former). Loeske (1906) reported observations taken from a single population of *Pohlia annotina* over a three year period and confirmed that the young propagula of this species are small and clustered in the leaf axils, but found that "relic" propagula which remain on the stems late in a growing season often continued growth, became quite large, and frequently occurred singly. It became clear that as a diagnostic criterion, having the propagula arranged in clusters versus singly was subject to variation within species, and was consequently of limited taxonomic value in distinguishing certain propaguliferous species. For some species, the distinction between small and clustered versus large and solitary propagula is invariably diagnostic. For example, *P. drummondii* never has small, clustered propagula at any stage of development. Young propagula are single (rarely 2) in the leaf axils and rapidly become large (400-1000 um long) and conspicuous. Vigorous stems of this species often have three to five large propagula scattered singly in the leaf axils and young propagula can be found only with dissection of the apical leaves. The young propagula arise singly, appear pale-green, but are fleshy and bulbiform with well developed, broadly laminal leaf primordia. They are otherwise similar, though smaller, to the larger propagula found lower on the stem. Propagula found just a few leaves below the stem apex are characteristically large, single, and bulbiform with a red pigmentation. A similar developmental situation is evident in *P. filum*, where the propagula also arise singly and are invariably large (350-650 um long) and bulbiform. The morphological distinctions between these two species are discussed in a later section.

Pohlia proligera, on the other hand, never produces large, bulbiform propagula and most herbarium specimens have clusters of linear-vermicular propagula in the upper leaf axils. Even when most propagula have fallen from the stem, those remaining are small, more or less linear, and vermicular. Bulbiform propagula have not been observed on stems in the field, on herbarium specimens (or lost in the packet), or on stems of cultured populations. In transplanted populations, propagula of *P. proligera* reach their characteristic clustered arrangement just three to five leaves below the apex and do not become large or bulbiform anywhere on the stem. Populations grown in a greenhouse from September 1977 until October 1979 have failed to produce bulbiform propagula at any time of the year. During the early spring in both field and greenhouse populations, the few propagula remaining attached to overwintering *P. proligera* stems are very similar, though often deeply transluscent red, to the propagula borne on young shoots of the current year.

Unlike *P. proligera* or *P. drummondii*, *P. andalusica* may have either or both types of propagula at various times of the year. Herbarium specimens of *P. andalusica* often contain stems with clusters of small (e.g. 150-300 um long) propagula, but the larger bulbiform type can frequently be found loose in the packet. Occasionally a complete sequence from the small obconic propagula to the large oblong, bulbiform types can be demonstrated on a single stem (fig. 5: 1-5). To add to the difficulties of adequately describing this species, it is not infrequent to find stems with only large, bulbiform propagula (cf. *P. drummondii*), although with a careful search of the loose debri in most herbarium specimens, the smaller, obconic propagula can also be found. In cultured populations of *P. andalusica*, the propagula invariably *arise* in clusters in from one to a few upper leaf axils (fig. 5: 5). It is only late in the growing season that these propagula may *appear* single in the leaf axils, this fact having been the cause of a great deal of nomenclatural confusion surrounding this taxon and *P. annotina*, where a similar situation of continual developmental change is present.

In *P. annotina*, as in *P. andalusica*, the propagula invariably arise in clusters, but may become few or single as the season progresses. This species exhibits a high degree of morphological variation with respect to its propagula; the young, clustered forms ranging from shortly obconic or triangular, to those which are long, narrow, and very gradually broadened to the apical end (away from its point of attachment to the stem). Superimposed on this between-population variation is a continual sequence of developmental changes within each population (see also Lewis & Smith 1977). As some propagula fall from the stems, those which remain often become longer, broader, and the leaf primordia become larger and sometimes broadly laminal in form (fig. 14: 12).

This parallel sequence in propagulum ontogeny from small and clustered, to large, single, and bulbiform has led to considerable misinterpretation of both *P. annotina* and *P. andalusica*. Ontogenetic convergence in morphology is not to be confused with actual intergradation between these two species however, and I have never encountered forms which could not be assigned to one or the other species with confidence. Character-states useful in distinguishing *P. andalusica* and *P. annotina* are given under *P. andalusica*.

Although culture studies (Lewis & Smith 1977, present work) have confirmed the reliability of propagula as diagnostic characters in distinguishing propaguliferous taxa, it is hopefully clear from the above discussion that care must be taken when describing the occurrence of propagula as diagnostic to a given taxon. The distinction between how a propaguliferous shoot may *appear* at certain times of the year and how the propagula actually *arise* is an important one, and this emphasizes that the propaguliferous

Pohlias should be defined on the basis of the species-specific *developmental pathways* which characterize their propagula.

Historical Survey of the Literature

The present discussion is intended as an historical account of the early literature of the propaguliferous Pohlias. Interpretations are purposely kept at a minimum, and nomenclatural discussions and conclusions are deferred to later sections (III & IV).

The Dillenian Era

During the Dillenian era, the epithet *annotina* (as given by Linnaeus 1753) was used without reference to propagula. The phrases of Dillenius, Linnaeus and other botanists of the early and mid eighteenth centuries included features of the gametophyte and habit of the sporophyte, and these were considered diagnostic criteria for recognition of this species. It is likely that botanists of the Dillenian era applied the name *Bryum (Mnium) annotinum* to species in the present genus *Bryum*, probably in the group designated "section 1" by Nyholm (1958) (see below).

In his *Historia muscorum*, Dillenius (1741) first used the name *Bryum* for a large, heterogeneous group of so-called acrocarpous mosses, and described *Bryum annotinum lanceolatum pellucidum, capsulis oblongis pendulis*. Dillenius divided his genus *Bryum* into *Ordo* I and *Ordo* II, based on the capsule being erect (*Ordo* I) versus pendulus (*Ordo* II), and subdivided these groups into "*series*" and "*divisios*" on the basis of both gametophytic and sporophytic (superficial) features. In his *Ordo* II, *Series* II (*species pendulae foliis angustis, mediocri latitudine praeditis*), *Divisio* II (*surculis et cauliculis inaequalibus*), he classified *Bryum annotinum* ... with eight other species. Within *Divisio* II, Dillenius distinguished taxa mainly on the basis of capsule shape and on the habit, shape, and texture of their leaves. *Bryum annotinum* ... was placed between *Bryum foliis latiusculis congestis, capsulis longis nutantibus* and *Bryum lanceolatum pellucidum, capsulis rotundis, pendulus carneis*. Thus Dillenius (1741) defined his species *Bryum annotinum* ... on the basis of its pellucid, lanceolate leaves and on its long pendulous capsules (p. 399) without reference to asexual propagula. In synonomy of *B. annotinum* ..., Dillenius referred to his earlier flora of Geissen, Germany (Dillenius 1719), and to Buxbaum's (1721) *Enumeratio plantarum... Hallensi....*

Figure 68 of *Historia muscorum* shows four sporophyte-bearing plants and eight unbranched gametophytes, two of which (fig. 68 E) are evidently perigonial plants. The four sporophyte-bearing plants appear with a central rosette from which three or four erect, sterile shoots arise, in addition to the seta. According to Lindberg (1883) there exists in the Dillenian herbarium a specimen labelled *Bryum annotinum lanceolatum pellucidum, capsulis oblongis pendulis*, which Lindberg determined as *Bryum pallens* Sw. (sic). This species is in every respect consistent with Dillenius' (1741) description and illustration of *B. annotinum* ..., and there is no reason to associate his species with any member of the propaguliferous complex in *Pohlia*. The rosette habit illustrated for *B. annotinum* ... in fig. 68 (1741), is much more indicative of a *Bryum* than a *Pohlia*.

In his publications of 1737 and 1745, Linnaeus did not refer to *Bryum* (or *Mnium*) *annotinum*. In his *Species Plantarum*, Linnaeus (1753) divided Dillenius' (1741) genus *Bryum* into *Mnium* and *Bryum*, and described *Mnium annotinum* with the phrase, *foliis acuminatis pellucidis, pedunculis subradicalibus, anthera nutante*. It can be seen that the description given by Linnaeus (1753) is essentially similar to that provided by Dillenius (1741), differing only with the addition of the information, "*pedunculis subradicalibus*", and by describing the leaves as "*acuminatus*" rather than "*lanceolatum*". Schimper (1871) reported that a specimen labelled *Mnium annotinum* in the Linnaean herbarium (LINN 1264.21) consists of two parts, the first part being *Ceratodon purpureus* Hedw. and the second, *Bryum cernuum* (sic). According to Savage (1945), this specimen bears the annotation "*Bryum*" by the hand of Dillenius. Although Linnaeus and Dillenius did meet during

Linnaeus' trip to Oxford in 1736 (Isoviita 1970), there is some question as to whether the specimen of *M. annotinum* in Linnaeus' collection could have been annotated by Dillenius. According to Isoviita (in litt.), this annotation (referred to by Savage 1945) was more probably written by O. Celsius (or a person assisting him) in Uppsala. Isoviita (1970) has discussed the care that should be taken when assuming that specimens presently in the Linnaean herbarium are automatically appropriate for typification of names credited to Linnaeus. Because of Linnaeus' herbarium techniques (re: discarding earlier specimens in favor of better ones acquired later, Isoviita 1970), it is often difficult or impossible to determine if a given specimen should be considered authentic, as opposed to being an appropriate neotype, at best. The specimen referred to by Schimper (1871) *may* be authentic. On the other hand, *Bryum cernuum* (= *Bryum uliginosum* B.S.G.) may well represent the taxon to which Linnaeus applied the name *Mnium annotinum* in 1753, especially since this species is morphologically similar (and phylogenetically related) to *Bryum pallens*, the species to which Dillenius (1741) apparently applied the name. Quite likely, neither Dillenius nor Linnaeus distinguished these two similar species. As to the sample of *Ceratodon purpureus* included in LINN 1264.12 (Schimper 1871), all bryologists know well how this species can turn up in unlikely places! It should be pointed out that Linnaeus (1753) also described a *Bryum purpureum* for which he provided a description consistent with *Ceratodon purpureus*, and that Schimper (1871) determined a Linnaean specimen so-named as *Ceratodon*. It would seem probable that Linnaeus was well aware of this ubiquitous species, and that its inclusion in LINN 1264.12 was simply one case of a mixed collection.

Following the publication of Linnaeus' (1753) *Species Plantarum*, other authors referred to *Mnium (Bryum) annotinum* with little change from the protologues of Dillenius or Linnaeus. For example, Hudson (1762) described *Bryum annotinum* with the phrase, "*antheris oblongis nutantibus, foliis ovatis acuminatis pellucidis, pedunculis subradicalibus*", this being a combination of the earlier phrases of Dillenius and Linnaeus. Likewise, Gunnerus (1772) referred to *Mnium annotinum* without mention of propagula. See Bridel (1803) for a thorough listing of eighteenth century references to *Mnium (Bryum) annotinum*.

The Hedwigian Era

Beginning with Leers' flora (1775), the occurrence of asexual propagula was included in the specific circumscription of *Bryum annotinum*. During the time of Hedwig, and well into the early nineteenth century, propagula were consistently employed in the description of this species, but no attempt was made to distinguish more than one propaguliferous taxon until Bruch, Schimper and Gumbel

(1839) described a propaguliferous variety of *Bryum ludwigii;* the variety *gracile*. During the Hedwigian era then, the epithet *annotina* was used in a modern, though inclusive sense, which included at least one of the present day propaguliferous species of *Pohlia*.

In his *Flora Herbornensis* (1775), Leers employed the familiar phrases of Dillenius and Linnaeus in his description of *Mnium annotinum; "foliis ovatis acuminatis pellucidis, pedunculis subradicalibus, antheris nutantibus"*. He then continued, "*individua juniora sterilia bulbifera: bulbilis purpureus subrotundis, pellucidis, solitaris, sessilibus in foliorum alis*". In synonomy of his *Mnium annotinum,* Leers referred to Linnaeus (1753), Weiss (1770) and Necker (1771). There is no illustration of *M. annotinum* in *Flora Herbornensis,* and a great deal of discussion has since focused on the possible identity of Leers' species (e.g. Warnstorf 1904, Loeske 1905, 1907, Buch 1906). According to Stafleu (1967) and Sayre (1977), Leers' herbarium has been lost or destroyed, and I have been unsuccessful in locating a specimen of *M. annotinum,* determined by Leers. In view of the discussion of developmental variation presented above, it is impossible to definitely identify the species to which Leers (1775) referred (he probably referred to more than one species in their modern sense). His description circumscribes a taxon in which single, more or less round, translucent, reddish propagula are present in the leaf axils (his phrase "*sessilibus in foliorum alis*" is in error since propagula of all the *Pohlia* species have a more or less obvious stalk). On this basis, it can be concluded that Leers referred to *Pohlia drummondii*, *P. filum*, *P. andalusica* and/or *P. annotina*, since each can have single propagula consistent with the description given for *Mnium annotinum*. Although the acceptance of Hedwig (1801) as the nomenclatural starting point for *Musci* renders the identity of Leers' *Mnium annotinum* irrelevent in a practical sense, I might suggest that his description of the propagula is slightly more consistent with *Pohlia annotina* (Hedw.) Lindb. than the other possible species. In particular, Leers referred to the propagula as "*pellucidis*", a character state which is much more pronounced in *P. annotina* than any of the other species with single propagula. See the section entitled "Recent nomenclatural arguments" for contrary opinions concerning the identity of Leers' (1775) *Mnium annotinum*.

Hedwig (1782) referred briefly to *Bryum annotinum*, listing several earlier works (including those of Dillenius 1741 and Linnaeus 1753) in synonomy of the species. He did not cite Leers' publication, although he did include the same literature citations (ie. Weiss 1770, Necker 1771) that Leers (1775) had. In this work, Hedwig (1782) did not refer to the presence of propagula, but judging from his comment in 1801 (Hedwig 1801 p. 185) that he had been aware of the species since 1773, it can be assumed that he intended the same plant in 1782 and 1801.

Roth (*in* Usteri 1794) described *Trentepohlia erecta*, in synonymy of which he referred to Oeder (1770), Oeder et al. (1761), Gunnerus (1772) and Ehrhart (1788). In 1800, Roth (1800a) placed *T. erecta* in synonymy of *Bryum annotinum*, and here discussed (p. 233) some of the early confusion which had surrounded this taxon. He indicated that many authors had interpreted fertile and sterile forms of *B. annotinum* to be different species, and credited Leers (1775) with clearly describing both fertile and propaguliferous sterile expressions of the taxon. Roth (1800a) further referred to a specimen collected by H.A. Schrader which contained both sporophytes and propagula-bearing shoots. He concluded that *Trentepohlia* Roth should be considered synonymous with *Bryum annotinum*, and consequently in his *Tentamen Florae Germanicae*, Roth (1800a) placed his own *Trentepohlia erecta* in synonymy of *Bryum annotinum*. In the *Miscellaneae* of his *Catalecta Botanica*, Roth (1800b) once again confirmed that his *Trentepohlia erecta* represented a sterile form of *Bryum annotinum*, and again referred to the Schrader specimen which contained both sporophytes and propagula. In fact, as soon as Roth realized that his moss genus *Trentepohlia* fell into synonymy, he described a new genus *Trentepohlia* (Cruciferae) in volume 2 (p. 73) of the "*Catalecta*" (Wagenitz in litt.)! In the herbarium of the University of Gottingen (GOET), there exists a specimen with the following annotation, "*Mnium annotinum cum surculis bulbiferis* (Trenthepol.) von H. Professor Schrader." The specimen (!) is a well preserved plant of *Pohlia filum*, containing both sporophytes and sterile, propaguliferous shoots. Unfortunately, the author of that annotation is not known (Wagenitz in litt.).

Meanwhile, in 1795, Hoffmann (1795) referred to *Trentepohlia erecta* Roth, describing the propagula as "*sessilia intra axillas foliorum, ovata*". In his plate 14, Hoffmann illustrated the plant, showing sterile shoots, perigonia, perichaetia and several propagula (fig. N & O). The propagula are oblong-sphaeroidal and have a cluster of laminal leaf primordia restricted close to the apex. These illustrations are very reminiscent of *P. filum*, including one (fig. O) which shows a propagulum with rhizoids and a young shoot emerging from the apical leaf primordia. Such partly sprouted propagula are not uncommon in specimens of *P. filum*, especially those which remain damp for some time after being collected. In the Hedwig-Schwaegrichen herbarium in Geneva, there is a specimen for which the annotation is only partly legible. It reads (in part), "*Trentepohlia erecta* Hoffm. ipse Hoffmann." This specimen (!) consists of sterile, propaguliferous shoots clearly referrable to *Pohlia annotina* (Hedw.) Lindb. Sporophytes are not present. In view of the contradictory nature of this specimen and Hoffmann's (1795) illustration, it can be assumed that Hoffmann, like other authors of the "Hedwigian era" did not distinguish what we today consider to be distinct, propaguliferous *Pohlia* species.

Hedwig (1801) provided a detailed description and excellent illustration of *Bryum annotinum,* adding to the familiar phrases of Dillenius and Linnaeus, and provided a discussion of the species' taxonomy. In synonomy of *Bryum annotinum,* he referred to the earlier works of Dillenius (1741), Linnaeus (1753), Roth (1794, 1800 b), Oeder *et al* (1761), Ehrhart (1788) and Hoffmann (1795), citing both *Mnium* and *Bryum annotinum,* and *Trentepohlia erecta*. In his discussion, Hedwig (p. 185) mentioned that he had observed this propaguliferous species since 1773 (see above), and described the plant saying that, "*saepe reperi aut intra plurimorum remotiorum, aut imbricatulorum summorum foliorum alas, proferre corpuscula* 2.3.4.5 *productionibus instructa, vid.* f.6.7." He went on to say that "*Bulbilli autem a* Rev. Trentepohl, *ipsius benevolentia accepti, foliolosi quidem erant* f.14. *at nihil continebant de relique.*" Finally, he added, " E. Cl. Hoffmanni fig. 1 c. *ad litt o. coniicere licet, oppressi aut laesi trunci gemmas esse, prodituræ innovationi servientes.*" Plate 43, illustrating *B. annotinum,* shows the plant's habit, including both gametophyte and sporophyte, and includes several drawings of microscopic features. Figures 6 and 7 show sterile shoots with clusters of small propagula in the upper leaf axils. Magnified illustrations of the "corpuscula" (marked "a" in his plate) clearly show obconic propagula with three to five peglike, apical leaf primordia, the diagnostic features for recognition of this species. Hedwig thus succeeded in illustrating the diagnostic criteria with which to identify his species, and his illustrations cannot be confused with any other species. *Pohlia proligera* is distinguished by its linear-vermicular propagula with only one or two leaf primordia, and *P. andalusica* by its propagula having conspicuous, broadly laminal leaf primordia. Figure 14, which Hedwig labelled "*Bulbillus ab ipso* Trentepohl *cum plantulis acceptus*", shows a small, leafy bud, interpreted by Hedwig to be a young branch bud (see Hedwig's discussion quoted above).

Two herbarium specimens labelled *Bryum annotinum* exist in the Hedwig-Schwaegrichen herbarium in Geneva (G). These two specimens were discussed by Loeske (1905), who concluded that both sheets contain an interspecific mixture. Upon examination of the specimens, I would agree with Loeske (1905) and Ruthe (who annotated the specimens) that in addition to *Pohlia annotina* (Hedw.) Lindb., the sheets contain both *P. andalusica* and *P. filum*. The two sheets each contain a series of shoots numbered consecutively from left to right. The first sheet (discussed in the same order as Loeske (1905) to facilitate comparison) has the notation in Hedwig's handwriting; "*Olim Chemnitzii sax. lectum*", and lists *Mnium annotinum* L. and *Bryum annotinum* Dill. as synonyms. Also included were the page and figure citations from *Species Muscorum*. This specimen was probably collected by Hedwig himself in the area of Chemnitz, where he had been practicing medicine since 1762 (Margadant 1968). My taxonomic interpretation of the numbered shoots is as follows:

1 *Pohlia annotina* (cf. fig. 14: 8)
2 *P. annotina* (cf. fig. 14: 2, 8)
3 *P. annotina* (cf. fig. 14: 1)
4 *P. andalusica* (cf. fig. 14: 11)
5 *P. annotina* and *P. andalusica* in mixture (propagula absent)
6 *P. annotina* and *P. andalusica* in mixture (propagula absent
7 *P. andalusica* (cf. fig. 14: 9)
8 *P.* cf. *andalusica* (propagula absent)
9-13 *P.* cf. *filum* (propagula absent)

Ruthe's annotation of the specimen reads: "1 bis 7 richtig *W. annotina* (Hedw.) Bruch, doch sind 2 und sterile aste unter 6 zu *W. rothii* Correns gehorig. β. *nivale* 9 bis 13 gehorig auf *W. gracilis* (Schleich.) Revid. D. Ruth 25, 11.04." As can be seen, Ruthe and I agree that in addition to *P. annotina auct.*, the herbarium sheet contains *P. andalusica (= P. rothii)* and *P. filum (= P. gracilis)* as well.

Numbers five and six are interpreted as a mixture of *P. andalusica* and *P. annotina* although propagula are absent in both cases. Each contains male and female plants and several sporophytes. There are two types of male plants present, some branched below the perigonia and others that are unbranched. The former character state belongs to *P. andalusica*, and the latter to *P. annotina*. Further, the unbranched plants have glossy, more or less erect leaves which are characteristic of *P. andalusica*, while the unbranched plants have dull, spreading leaves as in *P. annotina*. The sporophytes appear to belong to *P. annotina*. Number eight also lacks propagula, but I interpret it as *P. andalusica* based on the erect, glossy leaves. Shoots numbered 9 through 13 were distinguished on Hedwig's herbarium sheet as (var.) β nivale Hook. (number 11 is missing). According to Wilson (1855), Hooker (mss) referred to *P. filum* as *Bryum nivale*, and it is likely that the annotation, β nivale was added to this sheet after Hedwig's death. I agree with Loeske (1905) and Ruthe who felt that the shoots are probably *P. filum*. Propagula are absent, but the closely appressed, somewhat glossy leaves definitely indicate that they are *P. filum*. The quite shortly acute perigonial bracts of the male plants are consistent with the determination as *P. filum*. The bracts of *P. annotina* are notably long acuminate, and those of *P. andalusica* are variable, but usually longer than those of *P. filum*.

Hedwig's second herbarium sheet of *Bryum annotinum* has *Mnium annotinum* L., *Bryum annotinum* Dill., and

Trentepohlia erecta Roth listed as synonyms in Hedwig's handwriting. My interpretation of the numbered specimens is as follows:

1 *Pohlia annotina* (cf. fig. 14: 1, 8)
2 *P.* cf. *annotina* (propagula absent)
3 *P. andalusica* (cf. fig. 14: 11)
4 *P.* cf. *annotina* (propagula absent)
5 *P.* cf. *annotina* (propagula absent)
6 *P. annotina* (cf. fig. 14: 15)
7 *P. annotina* (cf. fig. 14: 8)
8 *P. annotina* (cf. fig. 14: 1, 2)
9 *P.* cf. *annotina* (propagula absent)

In spite of a few questionable interpretations of nonpropaguliferous shoots, it is clear that Hedwig's "type" specimens include a mixture of species. On the other hand, his description and illustration in *Species Muscorum* are referable to only a single taxon and thus provide the first unambiguous diagnosis for one of the propaguliferous species in *Pohlia*. From Hedwig's discussion of *B. annotinum* (see above) it is clear that he interpreted the propagula of *P. filum* (as illustrated by Hoffmann 1795 and Hedwig plate 43, fig. 14) as damaged, young branch buds, and thus conceptually he included the two species as one taxon; *Bryum annotinum*. The fact that *P. annotina*, *P. andalusica* and *P. filum* are included in his herbarium specimens of *B. annotinum* confirms that Hedwig did not conceptually distinguish the three, but this has no effect on the clarity of Hedwig's typification of *Bryum annotinum*. It is because of Hedwig's lucid drawings that the epithet *annotina* has been used in a consistent manner, at least in recent years.

During the early nineteenth century, authors following Hedwig (1801) cited the propaguliferous species as *Bryum annotinum* with various mention of the propagula diagnostic for this species. Hedwig (1801 and Roth 1800 a & b) had succeeded in clarifying the first source of confusion surrounding *B. annotinum*, i.e. that sterile and fertile forms were expressions of the same species. Bridel (1803) once again discussed the confusion between *Trentepohlia erecta* (sterile) and *Bryum annotinum* (fertile), listing the former as a synonym of the latter and providing a thorough list of eighteenth century references. It is worthy of mention that Bridel (1803) also described a *Bryum viviparum* within his section "*Brya incerta non genuina*", referring to Villars (1786-1789) in his protologue. Unfortunately *B. viviparum* is not represented by a specimen in Bridel's herbarium (Nowak *in litt.*), and further attempts at typifying the name have been in vain (specimens were requested from GREN, FT and H). If *B. viviparum* represents a present propaguliferous Pohlia, the name could be of nomenclatural significance.

During the following years, two new superfluous names were added to the synonomy of *B. annotinum*, but no new propaguliferous species were described. Lamarck and Candolle (1805) published *B. decipiens* with *B. annotinum* as a synonym, and likewise, Chevallier (1827) published the superfluous name, *B. bulbiferum*. In 1821, Schleicher

(1821) published *B. gracile* as a *nomen nudum* so that by the time Bruch, Schimper and Gümbel prepared their *Bryologia Europaea* (1836-1855), only one propaguliferous *Pohlia* species was known to science.

In 1839, Bruch, Schimper and Gümbel published *B. ludwigii* var. *gracile*, a propaguliferous form whose epithet they credited to Schleicher (1821). Their description and discussion (in which they noted that the variety was a dry habitat expression of the species) was accompanied by an illustration of the propagula. Their illustration (plate 14, fig. 9) is very characteristic of the species presently known as *P. filum*. In a letter dated September 1855 (ex herb Bruch - BM!), Wilson wrote to Bruch asking for a specimen of *B. ludwigii sensu Bryologia Europaea* because he thought that Schwaegrichen (who described *B. ludwigii*) had intended a different plant than that which was described by Bruch, Schimper and Gumbel (1839) as *B. ludwigii*. Apparently, Bruch et al. (1839) had been using *B. ludwigii* for a different plant, because in 1876, Schimper (1876) described *Webera commutata* to accomodate the plant referred to as *P. ludwigii* in *Bryologia Europaea* (see also under *P. drummondii* below). In that publication, Schimper retained the variety *gracile*, making the new combination, *Webera commutata* var. *gracile* (Schleicher *ex* B.S.G.) Schimper.

In North America during the 1820's, Thomas Drummond accompanied the Franklin land expedition to discover the elusive Northwest Passage (Bird 1967). As naturalist, Drummond collected Cryptogams in western Canada, later issuing the exsiccati set, *Musci Americani* (Rocky Mountains) from his collections. In 1843, Bruch and Schimper (in translation by R.J. Shuttleworth 1843) published a revision of Drummond's exsiccati numbers in which they commented on no. 263, which had been issued with the determination *Bryum nutans* var. *minor* Hook. (This name was never validly published with a description.) According to Bruch and Schimper, "The specimen marked A is *Bry. (Pohlia) acuminatum* var. *pulchellum*: and B is *Bry. (Cladodium) arcticum*; ...". Nearly twenty years later, Müller (1862 a) published the new species *Bryum drummondii*, basing the species on Drummond's no. 263. In his lengthy description accompanying *Bryum drummondii*, Müller made no mention of propagula, and described the capsule as "exannulata". In synonomy of *B. drummondii*, Müller cited Bruch and Schimper's (1843) *B. acuminatum* var. *pulchellum*, and in his discussion noted that "*quocum* Bruch *et* Schimper *commutayerunt, theca forma et folio laxe reticulato jam toto coelo distans* ...".

In that same year of the *Botanisches Zeitung*, Schimper (1862) quickly responded to Müller's suggestion that he and Bruch had confused Drummond's no. 263 with *Bryum pulchellum*. According to Schimper (1862), Müller was wrong in not one, but two respects. First, Müller (1862 a) was incorrect in considering his *Bryum drummondii* as new to science. Secondly, Müller was in error in assuming that Bruch and Schimper (in Shuttleworth 1843) had intended Hedwig's (1801) *Bryum pulchellum* as the basionym for their variety *B. acuminatum* var. *pulchellum.* To the contrary, explained Schimper (1862), it was on Hornschuch's (1819) *Pohlia pulchella* that they had based their new combination. Schimper went on to explain that his specimen of Drummond's no. 263 was clearly monoicous, and that *Bryum pulchellum* Hedw. is a dioicous species not even related to their variety.

During the next part of this rather spirited exchange between Müller and Schimper, Müller (1862 b) claimed "dass Hr. Schimper und nicht ich im Irrthum ist". Here Müller reasserted that his *Bryum drummondii* was, in fact, a new species. Further, he pointed out that Schimper must not have read his diagnosis of the species, which plainly stated that the plant was both "exannulata", and dioicous. Schimper had sent Müller a specimen which agreed closely with Schimper's sample of Drummond's no. 263, and Müller confirmed that it was not the same as that on which he had based *Bryum drummondii,* thus explaining the disagreement between the two authors. Müller then explained why he thought Bruch and Schimper had confused *B. drummondii* with *B. pulchellum* Hedw. Since *B. drummondii* was exannulate (according to Müller), his species was only comparable to *Bryum carneum* (sic), *B. albicans* (sic), and *B. pulchellum* (sic), the other three *Bryum* species which lack an annulus (Müller was incorrect with respect to both *B. pulchellum* Hedw., and his own *B. drummondii*, which do have annuli - see Demaret and Wilczek 1978). Müller reasoned 1) that since *B. drummondii* was clearly distinct from these three species, it had to be new, and 2) that since it was not even superficially similar to *B. carneum* or *B. albicans*, Bruch and Schimper (in *Bryologia Europaea*) must have conceptually confused it with *B. pulchellum* Hedw. Finally, Müller added that if he had assumed that Bruch and Schimper had confused *B. drummondii* with *B. acuminatum* (= *P. pulchella* Hornschuch), his criticism would have been even more harsh!

Demaret & Wilczek (1978) provided a thorough and interesting analysis of this problem and succeeded in locating the specimen of Drummond's no. 263 annotated by Bruch and Schimper (E). They compared it with duplicates of the exsiccati specimen in NY and at the British Museum (BM), and confirmed that it differed from these latter samples. Further, Demaret and Wilczek (1978) discovered that a specimen in the British Museum was annotated by Müller himself and appropriately designated it as the ectotype (specimen 263 c in Demaret and Wilczek 1978) of *. drummondii* C. Müll. Although Demaret and Wilczek (1978) onsidered *B. drummondii* as distinct from *W. commutata*, I can find no differences between the European material (i.e. *Pohlia commutata*) and the North American material (*P. drummondii*), and the two are consequently considered conspecific in this work. See the systematic treatment under *P. drummondii* for further discussion.

The Loeskean Era

Once the identity of *Pohlia (Bryum) annotina* as a propaguliferous taxon was firmly established during the Hedwigian era (ca. 1775-1865), the following decades of the nineteenth century brought several new species to science. It is worthy of note, that when Lindberg began to study the group in the 1860's and 1870's, *Pohlia annotina* and *P. filum* (as *W. commutata* var. *gracilis*) were the only two propaguliferous (Pohlia) taxa known. This era is named in honor of Leopold Loeske (1865-1935) who, although he did not describe any new propaguliferous species, was extremely instrumental in bringing some degree of stability to the previous taxonomic chaos.

In 1867, Lindberg reported *Bryum annotinum* Hedw. (sic) from Spitzbergen. The citation given for the two collections were *Bryum annotinum* Hedw. ♀ bulbilliferum, and *B. annotinum* ster. bulbilliferum; just as he annotated the specimens in his herbarium (H-SOL!). Both collections are actually *P. andrewsii*, an undescribed taxon endemic to the circumpolar arctic (see systematic section). When he published his "*Revisito Flora Danica*", Lindberg (1871) shifted

Bryum annotinum Hedw. to his new genus *Lamprophyllum*, making the combination *Lamprophyllum annotinum* (Hedw.) Lindb. There are two references to *L. annotinum* in Lindberg's "*Revisito*", one with reference to Oeder *et al* (1761) plate 215 (Lindberg 1871: 4), and the other with reference to Oeder *et al* (1858) plate 2613, figure 1 (Lindberg 1871: 75). In both cases, Lindberg cited the plants as *Lamprophyllum annotinum*, indicating that this was synonymous with *Webera annotina* (L.) Bruch (i.e. *W. annotina* (Hedw.) Bruch *ex* Schwaegr.). Also in 1871, Lindberg made the combinations *Lamprophyllum carneum, L. crudum, L. cucullatum, L. elongatum, L. longicolle,* and *L. nutans*. In 1879, he included these species in the genus *Pohlia*, again publishing new combinations. It is well known that Lindberg did not accept Hedwig's *Species Muscorum* (1801) as the nomenclatural starting point for Musci, and consequently he cited Linnaeus as the basionym author in his new combinations in *Pohlia*. Thus in *Musci Scandinavici* (1879), Lindberg listed *Pohlia annotina* (L.) Lindb., *P. cruda* (L.) Lindb., *P. nutans* (L.) Lindb., etc.

It seems clear that Lindberg used the name *Pohlia annotina* in 1879 for the same plant which he cited as *Bryum annotinum* in 1867 and as *Lamprophyllum annotinum* in 1871. It can be concluded then (at least with respect to Lindberg's intentions) that *Pohlia annotina* (L.) Lindb. (as cited in 1879) is nomenclaturally synonymous with

Bryum annotinum Hedw. (as cited in 1867). Because of the various opinions which have been put forward as to which presently understood propaguliferous species Lindberg intended as *P. annotina,* I have undertaken a revision of the material so named in Lindberg's herbarium. I have examined 49 specimens labelled *Pohlia* (or *Bryum, Lamprophyllum* or *Webera*) *annotina* from Lindberg's herbarium (H-SOL), all of which were incorporated into the collection before Lindberg's death in 1889. Of that collection, eleven are *P. andalusica,* nine are *P. proligera,* seven are *P. annotina,* six are *P. filum,* three are *P. bulbifera,* two are *P. drummondii,* seven are mixtures and four belong to the above mentioned, undescribed arctic taxon, *P. andrewsii*. From this evidence, it is clear that Lindberg used the name *Pohlia annotina* in a collective sense, including therein several presently accepted species which had not yet been described. There is no evidence to support the opinion (of e.g. Buch 1906, Koch 1951, Lewis & Smith 1978) that Lindberg used the name in an exacting sense for *P. rothii (= P. andalusica),* excluding Hedwig's *B. annotinum* from his concept of the species. It is true that many of specimens which Lindberg collected and identified as *P. annotina* from around Helsinki and southern Scandinavia are *P. andalusica,* but it must be remembered that this species was undescribed at the time, and can have propagula very similar to those of *P. annotina*. Lindberg, like

Hedwig, simply did not distinguish these two species.

Had Lindberg realized that he had been confusing several taxa under the name *P. annotina*, he surely would have described the unrecognized species. An interesting comparison can be drawn to his gradual recognition of *P. proligera* as a distinct species. J. Breidler began to send him plants labelled *Webera annotina* from Austria in the 1870's and early 1880's. Although they were apparently first included in Lindberg's concept of *P. annotina*, he soon began to realize that they differed consistently from other specimens to which he applied the name. By the early 1880's Lindberg distinguished these plants as the var. *micans* (Lindberg *in schedi*), and in 1887, he proposed a new name, *P. proligera* (in litt. fid. Kindberg 1888), to accomodate Breidler's specimens. Breidler also sent Lindberg other specimens that actually were *P. annotina* and Lindberg consistently included them within his concept of *Pohlia annotina*; i.e. a composite of at least *P. andalusica*, *P. annotina*, *P. filum* and *P. bulbifera*. There is no indication from his specimens that Lindberg ever recognized any distinction between *P. annotina* and *P. andalusica*.

Around the end of the last century and the beginning of the present one, there was a flurry of activity with respect to the propaguliferous Pohlias. After Breidler (1891) described *Webera proligera*, Warnstorf (1894) described *Webera bulbifera*, and the propaguliferous species, *Pohlia annotina*, became just one member of the propaguliferous complex. In a publication mostly overlooked by recent authors, Hohnel (1895) described *Webera andalusica* from the Sierra Nevada Mountains in southern Spain. An examination of an isotype of *W. andalusica* (FH-ex herb Schiffner) confirms this as a propaguliferous *Pohlia*, predating any other publication known to the author for this species (more recently referred to as *P. rothii*, e.g. Lewis & Smith 1977, 1978).

During the preparation of his treatise on asexual reproduction in mosses, Correns (1899) realized that many bryologists of his day were using the epithet, *annotina*, to include more than one species of propaguliferous *Pohlia* (Correns used *Webera* for the genus). He thought that in addition to *P. annotina sensu* Hedwig (1801, plate 43), bryologists were applying the epithet to an as yet undescribed species. He therefore proposed a name for the new taxon; *Webera erecta* A. Roth *ex* Correns, and suggested retaining *W. annotina* for the species which Hedwig had clearly illustrated. Correns referred to Roth's (1794) description of *Trentepohlia erecta* in his protologue and noted that the epithet, *erecta*, should be credited to Roth. However, he mentioned (1899 p. 160) that he had never seen authentic material from Roth's herbarium and in fact, admitted (p. 160) that he had not even seen Roth's publication. Correns went on to write that it was really Hoffmann's (1795) illustration of *Trentepohlia erecta* A. Roth that he had referred to when associating his species with Roth's. Hoffmann's illustration of the propagula from *T. erecta* agreed closely, according to Correns, with his collections from the Schwarzwald. As described above, Hoffmann (1795, plate 14, fig. M, N, & O) illustrated large, globose to oblong propagula borne singly in the upper leaf axils of his *T. erecta* plants. Correns (1899, fig. 95) similarly showed a plant with erect leaves and single, globose propagula as his *Webera erecta*. The illustration of *W. erecta* in Correns (1899) is quite characteristic of *Pohlia filum* (e.g. fig. 5: 9, 14: 14, present paper), and it is evident that the specimens which Correns himself had been incorrectly naming *Webera annotina* was this species. Lewis and Smith (1978) referred to a specimen cited by Correns in his protologue ("Vom Schwarzwald an der Strasse von Ruhstein gegen Achem), and according to Lewis (in litt.), the specimen is located in the herbarium of K.G. Limpricht (BP). Although I have not examined the specimen in Limpricht's herbarium, it is still possible, on the basis of Correns' characteristic illustration and detailed description, to confidently associate his species with *Pohlia filum*. *Webera erecta* is, therefore, taxonomically synonymous with *Pohlia filum*, a species published (as *Bryum* by Schimper 1876; lectotype: BM - Schimper!)

twenty-three years previously.

Shortly after publishing *Webera erecta* A. Roth *ex* Correns, Correns became aware that the name was predated by *Webera erecta* (Lindb.) Limpr. (a nonpropaguliferous species first described as a *Pohlia* by Lindberg in 1882, and later placed in *Webera* by K.G. Limpricht in 1892). Consequently, Correns wrote a letter to W. Limpricht, who was about to publish volume 3 of his late father's bryological treatise, and suggested a *nomen novum* to replace *W. erecta* A. Roth *ex* Correns. Limpricht (1902 pp. 728-729) reproduced Corren's letter as a footnote: "Als ich die bis dahin mit *W. annotina* Hedw. emend zusammengeworfene *Trentepohlia erecta* Roth als *W. erecta* wieder aufstellte, übersah ich dass es bereits eine *W. erecta* Lindb. (1883) gab. (conf. II. p. 239). Ich glaube, das hier #62 der "Lois de la nomenclature" in anwendung zu kommen hat und die Roth'sche art einen neuen namen erhalten muss. Ich schlage dafur *W. rothii* vor." It is clear from Correns' letter that *Webera rothii* Correns *in* Limpr. & Limpr. f. was intended as a substitute for an earlier name (*Webera erecta* A. Roth *ex* Correns) and must, according to article 7 of the ICBN, be considered homotypic with *Webera erecta*. In his protologue of *W. rothii*, Limpricht cited two exsiccata specimens; Breutel's *Musci Frondosi Exsiccata* no. 286, and Rabenhorst's *Bryotheca Europaea* no. 968. Both specimens in Limpricht's herbarium (BP!) are referable to the plant illustrated here as *P. andalusica,* as was noted by Lewis and Smith (1978 as *P. rothii*). However, as a *nomen novum, W. rothii* Correns in Limpr. & Limpr. f. cannot be said to have a "type", as such, but is typified by the type of the name it replaces; in this case, *Webera erecta* A. Roth *ex* Correns. I might add that Rabenhorst's no. 968 appears to have been a mixed collection, as that number in H-SOL and UC is *Pohlia annotina*. If one interprets *Webera erecta* as falling within the morphological range of *P. filum* (as I do), then *Pohlia rothii* must also be considered conspecific with *P. filum,* and in any event, even if typified by the specimens in Limpricht's herbarium, *P. rothii* is predated by *P. andalusica* (Hohnel) Broth.

As the epithets *gracilis* (as used by Bruch et al. 1839) and *filum* (as used by Schimper 1876) are considered to be taxonomically synonymous for the same species, it seems puzzling that Correns (1899) referred to two different species, *W. gracilis (= P. filum)* and *W. erecta (= P. filum)*. In fact, it seems obvious from Correns' discussion that he was very unclear as to just what the differences were between *W. erecta* and *W. gracilis*. In his discussion of *W. erecta,* Correns (p. 160) mentioned that of all the previously described propaguliferous Pohlias (Weberas), descriptions of *W. gracilis* came closest to agreeing with his new species, but that he was completely unfamiliar with *W. gracilis*. He went on to say that he had sent a specimen to Limpricht for his determination, and that Limpricht had called the plant *W. annotina*. This, of course, must have been what Correns had expected, since he thought the plant had previously been confused with *P. annotina*. He probably reasoned that if his specimen was actually *P. gracilis* or some other previously described species, Limpricht would have pronounced it so, and that Limpricht had not done so confirmed that his species was new! Under his brief discussion of *W. gracilis* (based on a specimen which Limpricht had sent), Correns (p. 167) remarked that "Die bulbillen dieser Art stimmen in allen wesentlichen Punkten ganz mit der *W. erecta* uberein, sie stehen ebenfalls einzeln in der Blattachseln (The bulbils of this species completely agree in all respects with those of *W. erecta;* which, in any case, occur singly in the leaf axils). It is not surprising, that in his figure showing the phylogenetic relations between the propaguliferous species, Correns (p. 158) placed *W. erecta* and *W. gracilis* very close together!

Finally, one might wonder; if *W. erecta* is the same as *Pohlia filum,* then where did *P. andalusica* (= *P. rothii* of later authors) fit into Correns' understanding of the propaguliferous Pohlias? Under *Webera commutata (= Pohlia drummondii)* Correns noted (p. 171) that he had received two specimens of this species from Limpricht, but that the two were somewhat different from one another. One of

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them had propagula occurring in clusters (specimen a) and was a slender plant, while the other had single propagula and the plants were more robust. Otherwise, Correns interpreted the propagula as being indistinguishable. Specimen a, apparently (I have not seen it), was *P. andalusica*, and Correns felt that this form with clustered propagula was conspecific with *P. drummondii*. This is a matter of taxonomic interpretation, and is beyond the scope of this section (see under *P. andalusica*).

It has seemed surprising to me, that even Loeske, who studied this group carefully in the early 1900's, did not immediately note that Correns (1899) had described the plant presently known as *P. filum* as his *W. erecta*. However, among some miscellaneous bryological notes in 1922, Loeske remarked that "Was Correns (Unters. ungeschl. Verm.) fig. 95 als *P. erecta* abbildet, passt nach Tracht, Blattform, Brutkorper so vollkommen auf *P. gracilis*, dass ich annehman mochte, ihm habe hier ein gemischte Probe vorgelegen" (What Correns illustrated as *W. erecta*, fig. 95, fits *P. gracilis* [= *P. filum*] so completely in habit, leaf-form and brood bodies, that I have to assume that he had a mixed sample) (Loeske 1922, p. 132).

Review of Recent Nomenclatural Arguments

Shortly after Correns' (1899) publication, a number of papers appeared in which the nomenclature of *Pohlia* *annotina* was discussed. In a meeting of the Societas Pro Fauna et Flora Fennica in 1899, H. Lindberg (1900) proposed the name *Pohlia grandiflora* for the propaguliferous plant illustrated by Hedwig (1801, plate 43), being of the opinion that *Pohlia annotina*, as applied by his father S.O. Lindberg (1879), was intended for a different species. The younger Lindberg, probably having examined his father's specimens collected around Helsinki, thought that S.O. Lindberg had used the name *P. annotina* exclusively for that species presently known as *P. andalusica (= P. rothii)*.

Warnstorf (1900) commented on Correns' *Webera erecta*, rejecting the species as synonymous with *P. annotina* since, Warnstorf observed, the latter species can have large, single propagula at some times of the year.

In 1901, Ruthe and Grebe (in Grebe 1901) described a new propaguliferous taxon, *P. annotina* var. *glareola*. Ruthe and Grebe distinguished their variety on the basis of its small stature and compact growth form, commenting that it agreed in all anatomical respects with typical *W. annotina*, including the form of its propagula. The type ("auf den Steinschutthalden der alten Kupferbergwerke bei Marsberg in Westfalen ... bereits 1893 (!), ... Juni 1897 (!) und 1898 (lectotype !)") is a compact, xeromorphic expression of *Pohlia andalusica*, not *P. annotina*. In 1902, W. Limpricht raised the variety to species rank as *Webera* *glareola*, and Brotherus (1903) made the combination in *Pohlia*. In none of these publications was *Pohlia glareola* compared to Correns' *Webera erecta*, since Correns had illustrated an entirely different plant in his "Untersuchen".

In the second edition of his "Kryptogamen Flora", Warnstorf (1904) followed H. Lindberg's (1900) nomenclatural reasoning, using the name *P. annotina* (Leers) Lindb. for the plant presently known as *P. andalusica* (= *P. rothii* of Lewis and Smith 1978), and replaced *Bryum annotinum* Hedw. with *P. grandiflora* H. Lindb. Warnstorf included a note (based on a letter from H. Lindberg) saying that S.O. Lindberg had replaced (L.) with (Leers) in his combination after becoming aware that Linnaeus' specimen of *Mnium annotinum* was something entirely different. This was the beginning of a rift among bryologists as to which species should retain the epithet *annotina*, and which should be given another name (i.e. *P. grandiflora* or *P. rothii* = *P. erecta*).

Loeske (1905) gave a thorough discussion of the problem, concluding that "*annotina*" must remain with Hedwig's plant, *P. rothii* being the correct name for the second species. His reasoning was thus. 1) Hedwig (1801) and Roth (1794) were the first authors to use propagula in the circumscription of propaguliferous *Pohlia* species. 2) Hedwig clearly described and illustrated *Bryum annotinum*

Hedw. 3) Roth intended a different species as his *Trentepohlia erecta* and thus Hedwig (1801) was the first to use *Bryum annotinum* in its modern sense (Loeske did later suggest in the same paper that Roth's *Trentepohlia erecta* might even be *P. annotina* with old, single propagula). 4) Lindberg's concept of *P. annotina* had been an inclusive one, and he did not exclude Hedwig's plant in his application of the name *Pohlia annotina*. On this point, Loeske pointed out that a specimen determined by Lindberg as *Lamprophyllum annotinum* and distributed by Brotherus was actually *P. bulbifera*, proving that Lindberg's concept had included several species. Consequently, concluded Loeske, the epithet *annotina* must remain with Hedwig's plant, but since Lindberg used the epithet for several species, Loeske suggested the combination *Pohlia annotina* (Hedw.) Loeske.

Buch (1906) replied to Loeske's arguments, making the following points. 1) Neither Roth nor Hedwig had first used propagula in describing *B. annotinum*, for Leers (1775) had employed them in describing *Mnium annotinum* in 1775 (see above). 2) Leers' description was the first unambiguous definition of the epithet, *annotina*, and Leers had intended the name for *Pohlia rothii* (= *W. erecta* A. Roth *ex* Correns), not Hedwig's species. 3) Lindberg did, indeed, have a clear concept of *P. annotina* (L.) or (Leers) Lindberg, since the plant is frequent around Helsinki.

Loeske (1907), after providing an interesting discussion of the variability of propagula in the propaguliferous complex, continued the preceeding nomenclatural discussion. Here Loeske asserted that 1) since Roth (1905) and other recent authors did not distinguish *P. annotina, P. rothii (= P. andalusica)* and *P. bulbifera*, how could Leers have, 130 years previously? 2) Leers may have been describing one of several species, judging from the description in Leers (1775), 3) Hedwig's type specimen typifies *B. annotinum*, and once that is done, the concept of later authors who publish new combinations (e.g. Lindberg) is nomenclaturally irrelevant. Finally, Loeske (1907) reasserted that the correct name for this species is *P. annotina* (Hedw.) Loeske.

Following these early discussions, Warnstorf (1913, in Bauer) described *P. hercynica*, based on Bauer, *Musci Eur. Exs.* no. 907. *Pohlia hercynica* was described in spite of Loeske's opinion (in Bauer 1913) that it was only a "luxurient Wasserform" of *P. rothii* (sic). The lectotype of *P. hercynica* (B-Warnst.!) is clearly conspecific with *P. andalusica*, and it is evident that most bryologists were still unclear about the differences between *P. annotina* and *P. andalusica* (then known as *P. rothii*)!

During the following decades, many Fennoscandian bryologists followed H. Lindberg's opinion and referred to Hedwig's *B. annotinum* as *P. grandiflora*, using *P. annotina*

(L.) or (Leers) Lindberg for the second species (= *P. andalusica* = *P. rothii* of earlier authors) (e.g. Brotherus 1923, Jensen 1939). For a number of years, the problem was not actively discussed, until Koch (1951) brought up the matter again, claiming that because Lindberg (1879) cited Linnaeus as the basionym author in his combination, and since Schimper (1871) had reported the Linnaean specimen so named to consist of *Bryum cernuum* and *Ceratodon purpureus*, Lindberg's combination must be rejected. Further, he argued that any combination made by Loeske citing Hedwig as the authority, must be considered superfluous and therefore be rejected. Koch argued that because we recognize Lindberg's other *Pohlia* combinations with Linnaeus as the authority, we cannot ignore his *Pohlia annotina* and accept Loeske's combination. Thus, concluded Koch, *Pohlia annotina* (L.) Lindb. should be considered synonymous with *Ceratodon* or *Bryum cernuum*, and he proposed using *Pohlia camptotrachela* (Ren. & Card.) Broth. (which he thought was conspecific with *Bryum annotinum* Hedw.) to replace *P. annotina* (Hedw.) Loeske. Koch's argument to reject *P. annotina* (L.) Lindb. (rather than simply substituting Hedwig's name for Linnaeus' as is done in Lindberg's other *Pohlia* combinations) was strengthened by his assumption that Lindberg had meant some plant other than Hedwig's when making the combination ("Modern bryologists agree that Lindberg (1879), the first to make the combination *Pohlia annotina*, did not use it for Hedwig's *B. annotinum*" Koch 1951 p. 258).

Margadant (1968) discussed Koch's (1951) paper, saying that "Here the [Koch's] reasoning is: since Lindberg did not cite Hedwig, he did not include his type in the concept of the species and it must automatically be excluded. This reasoning is open to doubt; it depends on the interpretation of the rules, and it can be reasoned that Lindberg cited Linnaeus only for brevity and that Hedwig would have been included, had he given a full list, in which case Hedwig's type would have been included under *Pohlia annotina* too."

Gradstein (1971) also discussed the problem, commenting that "The Index Muscorum (1965) follows Koch (1951) in rejecting the "confusing" name *Pohlia annotina* (Hedw.) Lindb. and replacing it by *Pohlia camptotrachela* (Ren. & Card.) Broth. The rejection of the name, however, has not been based on a study of the type of *Bryum annotinum* Hedwig which should be the legitimate basionym.... Hence, Koch's correction does not seem to be justified."

Wilczek and Demaret (1970) followed Koch's (1951) arguments and used *Pohlia camptotrachela* for the species, citing *Bryum annotinum* Hedw. as a synonym. Likewise, Lewis and Smith (1978) rejected Lindberg or Loeske's combination, saying that the name "had already been used by Lindberg (1879) for *P. rothii* (q.v.)."

Present Nomenclatural Conclusions

The present discussion is restricted to the nomenclature of *Pohlia annotina*. The situation with respect to the other propaguliferous *Pohlias* is reasonably clear-cut and will be discussed briefly under the section "Lectotypification" and in the systematic portion of this work.

As a result of the above literature survey and examination of authentic and type specimens, I can make the following observations, interpretations, and conclusions. 1) The pre-Hedwigian use of the epithet *annotina* (and the earlier phrases in which it was included) was extremely heterogeneous. During the so-called Dillenian era, *Bryum (Mnium) annotinum* was probably used for a member of the present genus *Bryum* (judging by the specimens in the herbarium of Dillenius and Linnaeus, fid. Lindberg (1883) and Schimper (1871) respectively). 2) During the Hedwigian era, *Bryum annotinum* was used for a broadly defined propaguliferous species with variable propagula (e.g. cf. fig. 14). Most authors of that time period probably used the name for more than one presently defined species, the application of any one author probably depending on which occurred in the geographic region with which he/she was most familiar. 3) Hedwig (1801) was the first author whose illustration and description can be definitely associated with a single, present species, and his type specimen includes that species, however in mixture. 4) Hedwig's (1801) *Species Muscorum* is the starting point for the nomenclature of Musci (ICBN Art. 13). 5) Lindberg (1879) made the first combination with the epithet *annotina* in *Pohlia*. 6) Lindberg used the name *Pohlia annotina* in an inclusive sense, not excluding Hedwig's *Bryum annotinum* in his use of the name, nor did Lindberg nomenclaturally exclude Hedwig's type in any of his publications. 7) *Pohlia annotina* (Hedw.) Lindb. is the earliest valid name for this species.

When arbitrarily setting a nomenclatural starting point date such as Hedwig's *Species Muscorum*, it is inevitable that there will be some discrepancies between pre- and post-starting point applications of some epithets (cf. Dixon 1933). My own opinion is that once such a date is agreed upon (e.g. Hedwig 1801), only a rather strict adherence to the rule (article 13, ICBN) can result in the intended nomenclatural stabilization. The code does allow that post-starting point names may be typified by pre-starting point references, though recommendation 32A suggests that such practice should not be favored. There is no direct provision in the code for the particular case of *Pohlia annotina* (Hedw.) Lindb., which (as Margadant 1968 noted) is open to interpretation of the rules. As Isoviita (in litt.) has pointed out, "... although Hedwig cited Linnaeus, the common agrument that "by changing the starting-point the type could be transferred from Linnaeus to Hedwig" does not automatically apply. Instead, the correct interpretation of Lindberg's nomenclatural practice may be more important ...."

With respect to Lindberg's nomenclatural practice, the question of importance is whether Lindberg intended to publish a new species (as *Lamprophyllum annotinum*) in 1871, or whether he was simply publishing a new combination. If he were intending a new species, not homotypic with Hedwig's (1801) earlier *Bryum annotinum,* then his name *Lamprophyllum annotinum* must be considered independently with respect to typification. If it is concluded that Lindberg did not exclude Hedwig's type when publishing *Lamprophyllum annotinum,* then the problem centers in the typification of the epithet, *annotina,* this typification fixing the nomenclature of both *Bryum annotinum* Hedw., and *Lamprophyllum annotinum* Lindb.

Evidence that Lindberg did not implicitly exclude Hedwig's type in 1871 (he definitely did not explicitly exclude it) comes from several sources.

1) In 1867, Lindberg actually referred to the plant as *Bryum annotinum* Hedw. Although this reference has no direct nomenclatural relevance, it does show that Lindberg did not intend to exclude the type of that name from his later publications (see discussion above).

2) When publishing *Lamprophyllum annotinum* in 1871, Lindberg

indicated that this species was synonymous with *Webera annotina* (L.) Bruch (sic). Although Lindberg did not actually refer to Hedwig here, the combination made by Bruch (ms., fide Limpricht 1892) was with reference to Hedwig as the authority. Again, since Lindberg did not explicitly refer to Hedwig in his own publication (1871), it could be argued that Hedwig's type was implicitly excluded, although I think Lindberg's intentions are clear. This is in full agreement with the remarks of Margadant (1968) and Isoviita (in litt.).

3) In their flora of northern Asia, Lindberg and Arnell (1890) cited the plant as *Pohlia annotina* (L.) Lindb., listing *Bryum annotinum* Hedw. as a synonym.

4) The specimens labelled *Pohlia (Lamprophyllum, Bryum, Mnium) annotina* in Lindberg's herbarium prove that he did not use the epithet in a narrow or restricted sense, excluding the plant described by Hedwig.

Given that Lindberg did not publish either *Pohlia* or *Lamprophyllum annotina* as a new species, then the Hedwigian epithet, *annotina*, must be typified. There are several possibilities for typification. Linnaeus' or Dillenius' specimens could be chosen since Hedwig (1801) referred to these authors in his protologue of *B. annotinum*, or a specimen from Hedwig's herbarium could be chosen. It is my opinion that the latter is most appropriate because: 1) Hedwig (1801) was the first author to use the epithet in a modern and definable sense, not Dillenius, Linnaeus, Leers, Roth, Hoffmann, etc. 2)Because of Linnaeus' practice of discarding specimens in favor of better ones obtained later (Isoviita 1970), there is no way to know if the Linnaean specimen referred to by Schimper (1871) or the Dillenian specimen referred to by Lindberg (1883) should be considered authentic and/or appropriate for typification of the epithet *annotina*. 3) Hedwig's specimens are authentic and appropriate, as indicated by the page, plate number, etc., from *Species Muscorum* in Hedwig's handwriting. 4) By virtue of the standing of Hedwig's *Species Muscorum* with respect to nomenclatural priority, it is advantageous to typify from his herbarium, whenever possible. 5) Typifying the name from Hedwig's herbarium is the only way to conserve current usage (by many authors) for the name *Pohlia annotina* (Hedw.) Lindb.

Suggestions for Lectotypification

Typification of the names of all the North American propaguliferous Pohlias is dealt with in some detail under the appropriate species in the Systematic section. Comments are made here only with respect to those critical species relevant to the present discussion.

Bryum drummondii C. Muller, Bot. Zeit. 20: 328. 1862. Demaret and Wilczek (1978) chose an appropriate lectotype bearing an annotation by the hand of C. Muller. Drummond, Musci Americani (Rocky Mtns.) no. 263 (BM-Hampe !).

Bryum filum Schimper, Syn. ed. 2: 470. 1876. Type: "... prope Chamounix (Payot)." (Lectotype: BM-Schimper !).

Webera andalusica Hohnel, AK. Wiss. Wien. Sitz. Math-Nat. Kl. 104: 326. 1895. Type: "am 28 September 1892 in circa 2800 m. Hohe an feuchten Orten subwestlich vom Picacho de Veleta in der Sierra Nevada ..." (Lectotype: FH-Schiffner !).

Bryum annotinum Hedw., Spec. Musc. 183. 1801. Type: "*Habitat locis arenosis argillosis, humidis, ad aggeres, fossas, aquas stagnantes continentes Germaniae*". Although no specific specimen was referred to in Hedwig's protologue, the specimen labelled "Chemnitzii sax. lectum" bears the plate and page numbers from *Species Muscorum* ... in Hedwig's handwriting. Article 70 (ICBN) allows selection of a single plant from a herbarium type sheet containing an interspecific mixture. The shoots labelled "1" on the above mentioned sheet have propagula in the leaf axils which agree closely with Hedwig's illustrations (plate 43, fig. 6, 7). (Lectotype: G-Hedwig-Schwaegrichen !).

Webera proligera Lindb. *ex* Breidl., Mettheil. Naturwiss. Ver. Steirmark 28.. 1891. Lectotype:"Schupfenberg bei Oblarn 12-1400 M" (GZU-Breidler !). I have examined nineteen of the twenty-four syntypes referred to by Breidler (1891). The lectotype is a handsome specimen bearing sporophytes.

EDAPHIC PREFERENCES AND GEOGRAPHIC ECOLOGY

Introduction

The Bryaceace is a large, ecologically diverse family of mosses which characteristically, although not exclusively, inhabit soil in open situations. Bryaceous mosses are often associated with high latitudes and altitudes, but given the large number of species in the family, they encompass an extremely wide variety of habitats. Species of the genus *Pohlia*, like most members of the family, typically occur on mineral soil and have their greatest North American diversity in the western cordillera. Among the approximately thirty North American *Pohlia* taxa, there exists a range of ecological preferences from *Pohlia nutans*, commonly found on rotting wood and *Sphagnum* hummocks at one extreme to *P. filum*, which is largely restricted to pure mineral soil, at the opposite end of the spectrum. Between these two extremes the species inhabit a continuous gradient of substrate types in terms of organic matter content, and the preferences of individual species are often narrowly and characteristically defined (see below). Some species (e.g. *P. crudoides, P. longicolla*) occur consistently in protected soil-filled rock crevices and are rarely found in the open on exposed soils, while most species inhabit sunnier habitats on tundra soil or along roadbanks or streambanks. The habitat preferences of most species are so characteristic that it is possible to reliably predict their occurrence once their preferences and geographic distributions are known. A few species (e.g. *P. ludwigii, P. cardotii, P. obtusifolia*) are almost totally restricted to alpine tundra soils and are frequent members of alpine plant associations wherever the bedrock is siliceous and the derived soil is mildly acidic to neutral in pH. Most species (including members of the propaguliferous complex) are characteristically found in somewhat protected pockets on soil banks bordering streams or lakes and are frequent along the banks of roads and paths.

Species in the sections *Lamprophyllum, Pohlia* and *Pohliella* most frequently grow on soil in which the pH is 4.5-6.0, and can be characterized as acidophilic, although they do occasionally grow on more calcareous soil. Members of the section *Mniobryum* are more calciphilic, often growing on soil of pH above 7.0, and are mostly absent from acidic areas. *Pohlia wahlenbergii* is a very common moss of moist, calcareous habitats, but this species will occasionally be found along streams in which the soil pH is between 5.5 and 6.0, and may co-exist with such mildly acidophilic species as *P. filum*. For the most part, however, members of the *Mniobryum* group are well defined ecologically and rarely co-exist with other members of the genus, even where the geographic ranges of several species from all four sections of *Pohlia* overlap. This kind of ecological differentiation makes the term sympatry difficult to define, since for all practical purposes, populations which are geographically sympatric are clearly allopatric with respect to the potentiality for interbreeding (Harper et al 1961 proposed the term synectic for the situation in which species are both geographically sympatric and co-exist ecologically).

Members of the propaguliferous complex are most common on soil of the 4.8-6.0 pH range, and each species exhibits an individualistic response to soil pH (see population data presented below). The most common habitat for the complex as a whole is on disturbed soil bordering roads and hiking paths and most of the species also occur in more "natural" habitats as well. *Pohlia andrewsii,* unlike any other member of the propaguliferous complex, is most frequent in the crevices among siliceous rock outcrops in arctic and/or subarctic-alpine tundra. It frequently co-exists with species such as *P. crudoides* and *Bartramia ithyphylla* Brid., and is uncommon on the more exposed tundra soil surrounding such rock outcrops where *P. drummondii* often occurs. On occasion, *P. andrewsii* is also found on roadbanks in north-central Yukon Territory and Alaska, but it is less frequent in such man-made habitats than are the other propaguliferous species. *Pohlia tundrae* and *P. drummondii* both frequently inhabit siliceous, alpine tundra soil, but also occur on roadbanks and other disturbed situations fairly frequently (especially the latter species). Just the opposite situation is true for *P. andalusica* and *P. camptotrachela*, which are most common along roadbanks, occurring occasionally but less frequently on tundra soil. *Pohlia annotina*, *P. proligera*, *P. camptotrachela*, and although generally less common, *P. bulbifera*, are the dominant mosses of roadbanks and pathbanks in siliceous areas, where they often co-exist with *Dicranella crispa* (Hedw.) Schimp., *D. grevilleana* (Brid.) Schimp., *D. shreberiana* (Hedw.) Schimp., and other ruderal species. *Pohlia filum* is quite specialized ecologically for habitats of low organic matter content (see below), and is most frequent on bare mineral sands and gravels along streams, especially along glacial streams where meltwater is constantly depositing new, organic-free sediments along its course. *Pohlia filum* is the dominant propaguliferous species colonizing gravelly roadside ditches in central Alaska.

It is apparent that the propaguliferous species each have two characteristic habitats, one in disturbed situations and the other in more "natural" habitats. It is logical to presume that in the absence of man-made disturbed habitats (which obviously have not existed for more than a relative instant in the evolutionary history of these species) members of the propaguliferous complex would be restricted to the natural habitats in which they are sometimes presently found. A consequence of this observation is that judging from the relative frequency of their occurrence in natural as opposed to disturbed habitats today, they must not have been as common in the past.

It is appropriate here to define, for the purposes of present discussion, several ecological terms which although are of common use among biologists, are applied with varying definitions by different authors.

Niche. Grinnell (1917) first used the term niche with reference to the ecology and distribution of the California Thrasher (Aves). Grinnel used the term in a physical sense to define the place which the thrasher occupied in relation to its association with other species in the California chapparal vegetation. Thus, Grinnel defined the thrasher's "ultimate associational niche", saying that it "is one of the minor niches which with their occupants all together make the chapparal association" (quoted in Whittaker, et al. 1973). Charles Elton (1927) used the term in a more functional sense, defining a species' niche (with reference to animals) primarily in terms of the food it eats, and thus linked the niche of a species to the trophic structure of the community which it inhabits. This application of the niche concept is exemplified by the work of Odum (e.g. 1953) who defined the niche in terms of a species' functional adaptations for procuring food in its ecological setting. Some later ecologists (e.g. Savage 1958) used the niche in such a functional context, more similar to the application of Elton than to that of Grinnell. Hutchinson (1958) formulated the modern niche concept, proposing that a species is affected by a set of environmental variables along a resource gradient such that within a certain range of that gradient the species is able to survive, but beyond which it is physiologically unable to exist. He further conceived that the shape of the so-called utilization function of the species along that gradient often takes the form of a normal distribution, with the species' potential for survival being greatest in the center (the physiological optimum) and gradually decreasing in either direction until the physiological limits are reached. Since a species is subject to, and affected by, many such environmental gradients simultaneously, Hutchinson (1958) suggested that the utilization function along these n gradients, define an n-dimensional hypervolume within which the species is physiologically able to exist. This abstract n-dimensional hypervolume may be visualized as a cloud-like form in which the frequency of resource utilization is greatest near the physiological optima, and decreases outward until the physiological limits are reached. This hypervolume may be termed the fundamental niche. Because no species lives in an ecological vacuum devoid of co-existing organisms, a species in nature is often excluded from a portion of its fundamental niche in which it could physiologically exist. The n-dimensional hypervolume defined by the environmental range in which a species actually does exist in nature is termed the species' realized niche (Hutchinson 1958, 1965), and is conceived of as a subset of the fundamental niche. It is important to realize that the center of the realized niche need not correspond to physiological optima, but only represents the species' most frequently inhabited place in nature in the context of its interactions with other species. The formulation of this niche hypervolume concept by Hutchinson was made with particular reference to Gause's (1934) "competitive exclusion principle", and to the co-existence of species within communities, and thus Hutchinson suggested (as did many authors before him considering the competitive exclusion principle) that no two species would inhabit precisely the same n-dimensional hypervolume; i.e. niche. The importance of Hutchinson's formulation is that it provides an operational definition of the niche, and allows one to measure niche parameters and test the competitive exclusion principle in an empirical manner.

The conceptual framework provided by Hutchinson (1958, 1965) is used presently for interpreting niche relations among the propaguliferous species in *Pohlia*. Although the niche concept as conceived in a functional sense (cf. Elton 1927) is entirely valid (especially in studies of animal ecology), it is of limited value in comparing niche relations among a group of congeneric plants of the same trophic level. Niche is therefore defined presently in a physical sense, being a measure of the kind of place a given species inhabits. It can be seen that the niche concept has little meaning except with respect to a particular species, and it is therefore not possible to speak of "empty niches", to be filled by an invading organism. Obviously, it is impossible to measure every one of the infinite (n) environmental gradients which characterize the niche hypervolume of a species. Often a few factors can be seen to be of overriding importance in determining the ecological distribution of a species, and a start can be made at quantifying a species' niche by measuring its resource utilization along these gradients. Root (1967) termed these critical environmental gradients the "adaptive core" of a species, and suggested that although co-existing species can tolerate considerable niche overlap without competitive exclusion occurring, it is this adaptive core which must be separated to allow for continued mutual survival of several ecologically similar species.

Habitat. This term is used casually by most botanists in a consistent sense to define the ecological setting which a species occupies in the overall landscape of a geographic region. That is, one speaks of the habitats of *Sphagnum* species as being rich, medium or poor fens, or of *Orthotrichum* species as being deciduous tree bark or rock surfaces. Whittaker et al. (1973) attempted to formalize the distinction between niche and habitat concepts, and their distinctions are of value in the present discussion. They pointed out that the niche hypervolume, as conceived of by Hutchinson is with particular reference to the place a species occupies in a single community (since Hutchinson was concerned with competitive relations of species which actually co-exist within a given habitat). That is, the niche hypervolume is defined by intensive, or with-in community environmental gradients. These gradients are then considered to constitute niche-gradients (Whittaker et al. 1973). In contrast to the intensive gradients, there are the so-called extensive, or habitat gradients. These are environmental gradients which vary over larger distances, such as elevation, slope exposure, etc., and the abstract hypervolume defined by the resource utilization of a species over these gradients may be termed the habitat-hypervolume (Whittaker, et al. 1973). When one wishes to consider simultaneously both niche and habitat gradients, Whittaker et al. suggest the term ecotope, and conceive of such an abstractly defined unit as the ecotope hypervolume.

The synecologist who is concerned with the organization of species into communities, and with problems of species co-existence, limiting similarity and competitive exclusion, is concerned primarily with subjects relating to the niche. On the other hand, the population ecologist or ecologically oriented systematist is concerned with a species' ecotope as the unit of ecological evolutionary change. Ecological distinctions between closely related species may take the form of niche differentiation or habitat differentiation, and differences in either (or both) habitat and niche constitute ecotope differentiation. For example, within the genus *Pohlia*, *P. nutans* and *P. cruda* can be said to be habitat differentiated since the former occurs primarily in the "rotting log habitat", while the latter occurs in the "soil bank habitat". Conceivably, two species may both occupy the soil bank habitat, but be niche differentiated on the basis of elevation specificity (which probably affects soil moisture) on a single such soil bank (see below). Hale (1974) reported that *Parmelia caperata* (L.) Ach. and *P. sulcata* Tayl. are differentiated along an intensive, elevation gradient on bark of the genus *Acer*. Thus, these two species of the genus *Parmelia* have evolved ecotope differences based on niche divergence, even though their habitats (*Acer* bark) are identical.

Two environmental gradients are presently being considered in relation to the frequency occurrence of populations of the propaguliferous Pohlias. The first ecological factor, soil pH, often varies considerably within a given habitat (Snayden 1962, unpubl. data), and thus constitutes a niche gradient along which species may be differentiated. It should be pointed out, however, that the pH gradient could be considered a habitat gradient, if considered in some other context with other groups of species. For example, *Pohlia nutans* grows most frequently on rotting logs which have a pH in the acidic range, although these logs may be found where the surrounding mineral soil is distinctly calcareous. In this case, *P. nutans* could be considered to be habitat differentiated from other species in the area, one critical factor determining its habitat being its position along the substrate pH gradient. The second ecological factor presently being considered is the per cent organic matter in the soil immediately underlying populations, and like pH, this gradient could be considered either a niche gradient or a habitat gradient in different contexts. It was qualitatively observed that the three basic habitats which these propaguliferous species occupy are tundra, roadbanks, and water-deposited gravel or sand, and these can be quantitatively defined by the organic matter content present in each. For this reason, the organic matter gradient may be considered to comprise the habitat hypervolume rather than the niche hypervolume. In one case, within the roadbank habitat, it was found that the vertical sides of the roadbanks consistently have a higher per cent organic matter than the frequently water-flushed gravels along the base, and this consequently constitutes a niche gradient within such habitats. *Pohlia camptotrachela* is often niche differentiated from *P. proligera* and *P. annotina* along this gradient, and rarely actually co-exists with them, although it may occur in the same habitat. That the distinction between niche and habitat gradients is sometimes not absolute does not detract from the value of conceptually distinguishing these ideas (as was noted by Whittaker et al. 1973). It should be added that no attempt was made to measure the fundamental niches of these *Pohlia* species, since all data were derived from field observations, and therefore species' distributions are those found when each is interacting with other community members, both congeneric and otherwise.

Central niche. Watson (1974) studied six species in the Polytrichaceae in order to quantitatively measure their utilization along selected gradients of the niche hypervolume (she selected light and substrate pH as the two gradients). In her presentation of the data, Watson compared what she called the "central niches" of those species, which she defined as the region along each resource gradient bounded by the mean ± 1 standard deviation of the values for each species. The central niche is thus a subset of the realized niche, comprising that portion of a resource gradient which a species utilizes most frequently, i.e. in qualitative terms, the most "typical" niche of a species. The central niche is presently defined as the smallest interval of the resource gradient within which thirty per cent of the populations of a given species are found.

Niche Breadth. A number of approaches have been suggested for the measurement of niche breadth (e.g. Colwell & Futuyma 1971, Roughgarden 1972). For present purposes, one standard deviation of the mean of a species population distribution along an environmental gradient was selected for its simplicity, and this value is considered sufficient for comparison of relative breadth of species' utilization of resources along such a gradient. Niche breadth is essentially a quantification of the concepts of specialist versus generalist when discussing the ecology of species. That is, a specialist has a narrow niche and a generalist has a broad niche. When defined in this way, it can be seen that describing a species as generalist or specialist is most meaningful when made with reference to a single environmental gradient, since any one species may be a specialist along one gradient while being a generalist along another. Consequently, it is of interest not only to compare niche breadth between species along the same gradient, but also to compare breadth of a single species along different gradients.

Niche breadth is controlled by complex and multiple factors, and is affected by such things as the rarity of resources along a gradient, and a variety of interspecific interactions. Roughgarden (1974) predicted (and provided supportive data) that niche breadth decreases with increasing productivity, and increases with decreasing competition. Root (1967) has pointed out that there are antagonistic pressures controlling the niche breadth of species. Interspecific competition for limited resources within a community implies selection for niche contraction, while intraspecific competition for resources may result in niche expansion. The niche relations among species in a community (and thus community structure itself) is the result of a compromise between these conflicting pressures.

The ecotope of a species may be considered the ecological expression of the species, just as its morphology is its structural expression. Most taxonomists define species on the basis of their morphological uniqueness, such that by definition, no two species have the same morphology. By the same token, if our morphologically defined species have biological meaning, it follows that no two species have the same ecotope. Modern community ecology is based on this idea of species ecological individuality (Gleason 1926), and this also forms a common theoretical basis for evolutionary biology and synecology. That is, a community may be conceived of as an aggregation of evolutionarily dynamic species populations distributed individualistically along environmental gradients (Whittaker 1967, 1969, 1970). One who is interested primarily in synecological problems may study species' relations to one another (in terms of diversity, etc.) along environmental gradients, while the evolutionary biologist may utilize the same data, but focus on individual species of interest, in terms of their ecological expression. For example, Whittaker (1956), using data derived from community sampling, constructed a two-dimensional habitat diagram for *Quercus prinus* L. which illustrated the ecological individuality of this species in the Great Smoky Mountains, Tennessee. In a similar manner, Hutchinson (1970) constructed the niche expressions of three species of aquatic angiosperms in the genus *Myriophyllum* using data collected for limnological studies of freshwater vegetation. Hutchinson's data clearly showed the ecological individuality of these three congeneric species, providing valuable data with respect to the structure of communities in which they occur, as well as providing additional data which can be useful in assessing the taxonomic status of the species. Vitt and Slack (1975) ordinated species along environmental gradients in *Sphagnum*-dominated kettle hole bogs, and found each to be distributed individualistically with respect to the niche gradients that they measured. Species in the genus *Sphagnum*, although commonly occurring in intra-generic mixtures of high species diversity, are clearly niche-differentiated within a common (bog) habitat. This ecological specificity is often invaluable in determining *Sphagnum* specimens (Vitt, verbal communication), and *Sphagnum* represents an excellent group for studying niche relations of congeneric species. Alpinis and Dioques (1933) and Alpinis and Lacis (1934) documented the pH preferences of a range of bryophytes and Ochi (1959 b), and Ochi and Mizushima (1963) reported similar data for selected species in the Bryaceae and Bartramiaceae, respectively. Ochi (1959 b) found that most species in the Bryaceae are "broad-adaptive" mosses in their relation to the pH gradient, but also suggested that certain more narrowly adaptive species (i.e. having a narrow niche breadth) in the genus *Pohlia* may have considerable indicator value by virtue of their niche specificity. The present study was undertaken to 1) document the potential indicator value of the propaguliferous species in *Pohlia* for soil characteristics and 2) to document the biological meaning in terms of edaphic occurrence of these species as they are defined on morphological criteria.

Materials and Methods

A total of 293 soil samples were gathered in conjunction with the collection of herbarium specimens for morphological study. Collections were made during the summer of 1978 over a large geographic area in western North America, ranging from south-eastern Alaska to Oregon and Colorado in the western cordillera. Soil was gathered from the surficial 2-4 cm. immediately underlying *Pohlia* populations and should represent surface soil characteristics as encountered by a colonizing and/or growing population. Five grams of each sample was measured for hydrogen ion concentration (pH) using a Beckman Electromate pH meter in a saturated soil paste consisting of soil plus distilled water. An additional portion of each sample from which pH had been measured was analyzed for per cent organic matter using the "wet combustion" method described by Sims and Haley (1971). Four populations (two of *P. proligera* and two of *P. drummondii*) were collected on decaying wood, and these were excluded from the statistical treatment of organic matter data. While these are noteworthy occurrences, they are definitely ecologically atypical and inclusion of them in the quantitative data modifies the descriptive statistics of resource utilization for these species such that they are rendered all but meaningless. A total of 289 populations were consequently measured for organic matter content.

Statistical comparisons of species' resource utilization along gradients of pH and organic matter content were made by comparison of population distributions rather than on the basis of differences in population means. Important niche (and habitat) differences between species often take the form of differences in the proportions of resources utilized along a common gradient, even where the species exploit essentially the same resources (Colwell & Futuyama 1971, Hutchinson 1965). Consequently, it is considered that comparing utilization distributions is a more useful test of niche differentiation than comparing a simple location estimate such as the population mean. The Wilcoxon signed-rank test (Dixon & Massey 1969) was employed for comparing resource utilization curves because this nonparametric test makes no assumptions concerning distribution shape. Two dimensional diagrams showing utilization along pH and organic matter gradients simultaneously were constructed for each species (e.g. fig. 18). Some mention of their construction is appropriate here so that their interpretation is clear. The outer circle of each figure is defined by four points; two point delimiting the range of soil pH on which 90% of the populations of that species occur (vertical axis), and two points delimiting the same range in terms of organic matter content. The 90 percent range is the central 90%; i.e. the maximum 5% values are excluded as are the minimum 5%. The middle circle (black vertical lines) delimits the 50% range of the two gradients, and the innermost circle (solid black) represents the central 20% range of values. The two gradients, organic matter content and pH, are not correlated so these figures *do not represent scatter diagrams* in which the circles delimit areas of decreasing density of occurrence. In the diagram for *P. filum*, for example (fig. 20), a population growing on soil with 1.3% organic matter (within the black innermost region) did not necessarily have a pH between 5.6 and 5.8 (also within the black circle). Because the two gradients are independent, a soil sample with 1.3% organic matter could have had a pH anywhere in the total range for that species (4.99-8.09). Thus, it is incorrect to say that 20% of the populations of *P. filum* grew on soil with the pH between 5.6 and 5.75 *and* with an organic matter content between 1.2 and 1.4. The correct probability that that statement is true is 4% (i.e. the probability of the two independent events occurring). The value of these figures is in comparing the utilization breadth of a species in relation to the two independent gradients. For example, it can be seen from the figure for *P. filum* that this species occurs over a narrow range of organic matter content as compared to its broader occurrence on soil of varying pH. Contrast this to the figure for *P. annotina* (fig. 25) which is more variable along the organic matter gradient than the pH gradient. The decision to connect the four points delimiting each range of percentage occurrence by rounded lines was an arbitrary one; the figures could just as well have been drawn as concentric squares. The choice was for aesthetic reasons, because the figures are only intended as a means for gross comparisons between species.

Results

In the present section, the occurrence of propaguliferous Pohlias in relation to environmental gradients is discussed, and the ecological preferences of each species is summarized.

P. drummondii: Pohlia drummondii has the highest mean per cent organic matter content in its substrate of any species investigated (2.35), except for *P. tundrae*, with which it frequently co-exists. Its central niche along the organic matter gradient is in the 2.25-2.70 range, indicating that its most typical habitat in terms of frequency population occurrence is in relatively humus-rich tundra situations. In rich subalpine habitats, where competition which vascular plants is probably keen, *P. drummondii* is frequently restricted to the banks of small streams. In such instances, it generally occurs on rich, more or less organic banks, and it is very infrequent along glacial streams where there is a constant build-up of loose, inorganic alluvium. In alpine situations, *P. drummondii* is found mostly in the middle alpine zone where plant cover is more or less continuous. When the tundra has been disturbed by motor vehicle tracks, *P. drummondii*, along with *P. tundrae*, is a frequent colonizer. In lowland to montane situations, *P. drummondii* occurs fairly frequently along pathbanks, roadbanks, and along moderately humus-rich streambanks. In figure 17, it can be seen that in addition to its primary occurrence on soils with 2.3-2.7% organic matter (alpine tundra), there is a secondary region of high frequency in the 2.0-2.3% range, and this corresponds to such roadbank habitats, where *P. drummondii* sometimes co-exists with *P. tundrae*, *P. proligera*, *Bryum creberrimum* Tayl., etc. Only infrequently does this species occur on sandy stream margins with a lesser degree of organic matter content (1.0-1.5 range in figure 17). On several occasions, I have collected *P. drummondii* on rotting wood, and at which time it was found on logs in the final stages of decomposition.

From figure 18, it can be seen that *P. drummondii* has approximately the same amplitude in relation to soil pH and per cent organic matter. The distribution of *P. drummondii* populations along the pH gradient is more symmetrical in form (fig. 17), extending over the range 4.40-6.70, but is centered in the 5.47-5.78 range (the central niche as defined above). In Alberta, *P. drummondii* occasionally occurs in calcareous alpine tundra, where it often produces numerous sporophytes, but few propagula.

P. filum: *Pohlia filum* is a most distinctive species ecologically, and is very predictable in its occurrence.

It is most frequent along the sand and/or gravel banks of streams or lakes, occasionally growing on dunes, on bare glacial moraine deposits or other areas of a similar inorganic nature. Along the organic matter gradient, it occupies a characteristic position in the 0.9-1.7% range, and the value for its niche breadth (0.31) along this gradient is the lowest of any species along either gradient (Tables 2,3). Only *P. camptotrachela* shows a similar affinity for organic-poor substrates, but the geographic distributions of the two species scarcely overlap. However, in British Columbia, Washington and Oregon, where the two species are sympatric, they sometimes grow intermixed along streams or at the bases of roadbanks. *Pohlia filum* shows a notable affinity for recently glaciated areas, being particularly frequent on inorganic outwash along braided streams or other geomorphic features associated with glacial meltwater. At sea level along the panhandle of Alaska, *P. filum* is common and often occurs as an extensive ground cover in front of the many presently receeding glaciers in that region. During the late Pleistocene, when such glacially induced habitats were more widespread in North America, *P. filum* was probably also more frequent and widespread. Quite possibly, *P. filum* could have migrated across North America at the foot of the retreating ice, although the high pH of much of these inorganic sediments could also have restricted migration to some extent. In a sense, *P. filum* can be thought of as existing in present day, relatively restricted "glacial refugia", where it can weather these inhospitable interglacial times until a renewed glacial episode occurs! The present distribution of *P. filum* is probably controlled in part by its edaphic limitations, and it only occurs in areas of North America which were glaciated during the Pleistocene. It has not been collected in the Rocky Mountains south of the Canadian-U.S. border (fig. 37), and this probably reflects, at least in part, the relative restriction of glaciation in the central Rocky Mountains and consequently also the kinds of sedimentary landforms that are so produced.

Along the pH gradient (fig. 19), *P. filum* is more broadly distributed, occurring on soils from pH 4.9-7.0. Its central niche along the pH gradient is pH 5.52-5.85, and its niche breadth (0.62) is the highest of any species along this gradient (table 2). As can be seen from figure 20, *P. filum* is much more narrowly limited along the organic matter gradient than the pH gradient, and its distribution along the latter is asymetrical, with more populations above the mean than below. *Pohlia filum* is similar to *Bryum pallens* (Brid.) Sw. *ex* Roehl. in its pH tolerance, but although the two often co-exist, *Bryum pallens* occupies an even broader range of soil pH (unpubl. data). *Bryum pallens* often co-exists with *P. annotina* on soil of pH around 5.0-5.5, with *P. filum* on soil around pH 6.0, and with *P. wahlenbergii* on soil of pH 7.0-8.0. On soils in the neutral pH range, *P. filum* sometimes also co-exists with such calciphilic species as *Aongstroemia longipes* (Somm.) B.S.G. or even *Pohlia vexans* (Limpr.) H. Lindb.

P. tundrae: Pohlia tundrae is a characteristic alpine moss in the western cordillera of North America. It usually occurs from just above treeline to the upper limits of more or less continuous vegetation, being a common member of middle alpine plant associations. The distribution of *P. tundrae* populations along the organic matter gradient (fig. 21) shows a maximum frequency in the 2.5-3.0% range, but with a greater number of populations below this region than above. The central niche of *P. tundrae* (OM = 2.30-2.65%) is essentially identical to that of *P. drummondii,* being the characteristic percentages found in the tundra soils on which they frequently co-exist. Also like *P. drummondii,* the distribution of *P. tundrae* populations along the organic matter gradient is asymmetric with more populations below the mean than above, this reflecting its occurrence along sandy roadbanks, where the organic matter content ranges from about 1.6 to 2.2 per cent. *Pohlia tundrae* does not occur on quite so organic-poor substrates as *P. drummondii* very occasionally does, and its distribution along the gradient shows a slightly narrower breadth (fig. 31). The difference in distribution, however, is not significant (Table 4). Along the pH gradient, *P. tundrae* is roughly symmetrical in its distribution (fig. 21), having its central niche in the 5.42-5.79 range. As noted above, *P. tundrae* and *P. drummondii* are practically indistinguishable ecologically, although the niche breadth of *P. tundrae* is slightly narrower along both gradients (Tables 2, 3).

Both *P. tundrae* and *P. camptotrachela* have geographic distributions centered in the western cordillera of the United States (fig. 41, 56). In comparing distributions of the two, however, it can be seen that *P. tundrae* has been collected frequently in Utah and also a few times in Nevada, while *P. camptotrachela* is unknown from either state. I do not think that this is a collecting artifact, but rather that it reflects a greater continental tendency on the part of *P. tundrae*. This species is rather common in the Rocky Mountains, but is less frequent, though not rare, in the Cascade-Sierra Nevada Ranges. *Pohlia camptotrachela* is by far most common in the Pacific coast region, occurring sporadically in the Rocky Mountains at high altitudes (see under *P. camptotrachela* for further discussion).

Pohlia andalusica: The ecological data for this species consist of samples from seven populations, and can thus only provide a crude picture of its distribution along the two gradients (fig. 23). PH measurements range from 5.12 to

6.69, and indicate that *P. andalusica* is probably rather broadly adapted to this environmental factor. Organic matter values range from 1.85-2.85, from which few conclusions can be made, although they are considerably higher than the average values for *P. filum* or *P. camptotrachela*. In western North America, *P. andalusica* is encountered in upper montane to low alpine habitats, but seems to be nowhere common. It is sporadically distributed in the western cordillera, and usually occurs as small, inconspicuous populations on mesic tundra soil or rarely along the sides of roads. *Pohlia andalusica* is far less common than *P. tundrae* or *P. drummondii* in alpine situations, and tends to occur on somewhat less organic-rich substrates, sometimes on small exposures of mineral soil among more densely vegetated tundra. In the Yukon Territory, *P. andalusica* sometimes occurs as a few, scattered, minute plants on frost boils of mineral soil exposed by freeze-thaw phenomena, and occasionally co-exists with *Bryum bicolor* Dicks. (s.l.), which sometimes occurs as similar depauperate populations in these habitats. In montane situations in the western Cordillera of British Columbia, Alberta and the United States, this species is found infrequently along roadbanks, etc., where humus accumulation is limited, generally growing at the base of such roadbanks rather than in soil pockets of the banks themselves, where *P. proligera* is more frequent. In the west, *P. andalusica* is not a common, weedy species, while in eastern North America it is more frequent in disturbed habitats such as roadside ditches, etc., and frequently co-exists with *P. bulbifera* and *P. annotina*. According to Loeske (1905) and Grebe (1901), *P. andalusica* also occurs as a roadside weed in central Europe, especially in Germany where they collected most frequently (as *P. rothii* and *P. annotina* var. *glareola*, respectively). Lewis and Smith (1978) noted that this species (as *P. rothii*) is sometimes associated with old copper mines in the British Isles, and Grebe (1901) stated that the syntypes of *P. annotina* var. *glareola (= P. andalusica)* were collected among the rubble of an old copper mine in Westfalen, Germany.

P. bulbifera: No quantitative data is available for this species although soil samples were collected from the Yukon Territory and Alaska during the summer of 1979, and results are forthcoming. *Pohlia bulbifera* is quite rare in western North America, but has been collected occasionally along roadbanks and in other disturbed habitats in the mountains. In the Yukon Territory and Alaska, this species is slightly more frequent than farther south, occurring along roadbanks or on the margins of lakes, often where the soil is strongly compacted for one reason or another. It has been collected several times in such exposed habitats as the margins of playgrounds or city paths where the soil is compacted almost to the consistency of cement. In eastern North America, particularly in the Adirondack Mountains of New York state, and in New England, *P. bulbifera* has been collected far more frequently than in the west, occurring along lakes, roads and/or streams where it often co-exists with *P. annotina* and *P. andalusica*. Although no quantitative data are available, it is clear from the occurrence of *P. bulbifera* on soils where the bedrock is siliceous that this species has pH preferences in roughly the same range as the other propaguliferous species.

P. annotina: Within its geographic range, *P. annotina* occurs frequently along the banks of roads, footpaths, streams, lakes,etc. Along the organic matter gradient (fig. 24), *P. annotina* has the widest amplitude of any species along either gradient (Tables 2, 3). Its distribution on soils of varying organic matter content appears somewhat bimodal in form, with a region of high frequency in the 0.9-1.4% range, and a second in the 2.2-2.6 (-3.0)% range. The 2.2-2.6% range represents its typical habitat on sandy, more or less stabilized roadbanks where it often occurs in protected depressions and under overhanging roots, rocks, etc. The lower values of organic matter content (0.9-1.4%) represent its occurrence along the bases of such roadbanks where running water periodically flushes out much of the loose organic matter. These latter habitats are similar to those in which *P. camptotrachela* are found, and the two species occasionally co-exist where their geographic ranges overlap (which is limited in North America). *Pohlia annotina* and *P. proligera* have similar distributions along the organic matter gradient, and qualitatively they occupy very similar roadbank habitats, although *P. proligera* typically occurs on soils of higher pH. The geographic ranges of *P. annotina* and *P. proligera* scarcely overlap in North America (fig. 52, 60), and the former species tends to be distinctly sub-oceanic in its distribution. *Pohlia annotina* is widespread in eastern North America where there is ample rainfall and the summers are relatively humid, but becomes less frequent in the mid-western states as the climate becomes more continental. It is abundant in the Smoky Mountains (southern Appalachians) and in the Adirondack Mountains of New York state where higher elevations cause rainfall to be particularly high. In western North America, *P. annotina* is distributed along the Pacific coast northward through Washington, British Columbia, and southern Alaska, but is absent or rare in the interior portions of these states and province. In Alaska, where there is a dramatic climatic gradient of decreasing rainfall from south to north, *P. annotina* is restricted to within 60-100 miles of the southern coast; and is absent from the central and northern portions of the state, as it is from the Yukon Territory. A similar sub-oceanic distribution appears evident for European populations of *P. annotina*, where it seems to be distributed widely in the British Isles and around the Mediterranean Sea. In contrast to *P. annotina*, *Pohlia proligera*, occurs widely in the interior portions of North America and shows no affinity for oceanic regions. A.C. Crundwell (in litt.) has confirmed that based on specimens determined by Warburg, and later, those determined by Crundwell using Warburg's criteria, *P. proligera* is restricted to the more continental areas of the British Isles than is *P. annotina*. Judging from numerous specimens in the herbarium of Crundwell, *P. proligera* is quite rare in the British Isles, and *P. annotina* is the commonly occurring member of the pair. A similar situation is evident along the Pacific coast of North America, where *P. annotina* is frequent relative to the occurrence of *P. proligera*. Further, *P. proligera* occurs widely in the continental Rocky Mountains, while *P. annotina* is known from a single locality at the base of Mt. Robson, British Columbia. Other oceanic species such as *Thuja plicata* Donn also extend eastward to Mt. Robson. *Pohlia annotina* also occurs at a few interior stations in Idaho and western Montana just west of the Rocky Mountains where other Pacific coast mosses such as *Ulota obtusiuscula* C. Mull. & Kindb. *ex* Macoun & Kindb., *Orthotrichum lyellii* Hook. & Tayl. (Vitt 1973), *Dicranum pallidisetum* (Bailey) Ireland and *D. sulcatum* Kindb. (Peterson 1979) are known to occur.

Along the pH gradient (fig. 24), *P. annotina* is centered in the 5.27-5.73 range, and has the lowest mean value of any species measured (Table 2). It is noteworthy that *P. proligera* has the highest mean soil pH of any species measured. In the Rocky Mountains of Alberta, where the mountains are highly calcareous and the climate strongly continental, *P. annotina* is absent but *P. proligera* occurs sporadically. Figure 25 shows that *P. annotina* occurs on substrates varying more in organic matter content than in pH, but this is partly because of its bimodal distribution along the organic matter gradient, which appears as a continuous spread in this figure.

P. andrewsii: No quantitative data are yet available for the ecology of *P. andrewsii*. Unlike other North American propaguliferous Pohlias, the typical habitat of *P. andrewsii* is in the soil-filled rock crevices in arctic or subarctic-alpine tundra. It very frequently co-exists with *P. crudoides* and occasionally *P. longicolla* in these habitats, and does not grow intermingled with other propaguliferous species which occupy more exposed situations. In the Yukon Territory and Alaska, *P. drummondii* is a common moss of the same tundra localities in which *P. andrewsii* is found, but because of their habitat differentiation, the two do not occur intermixed. It can be inferred from *P. andrewsii*'s occurrence in protected rock crevices, that it is able to tolerate lower light intensities than most other propaguliferous Pohlias. North American reports of *P. annotina* from arctic regions should be referred to *P. andrewsii,* which replaces the former species in these high latitudes with a continental climate. See under *P. andrewsii* in the systematic section for the morphological distinctions between these two species.

P. proligera: Like *P. annotina, P. proligera* is most frequent along roadbanks, pathbanks, ditches, or other man-made habitats. Its distribution along the organic matter gradient is similar to that species', but is less bimodal in form (fig. 26). The central niche of *P. proligera* (Table 3) along this gradient is 1.90-2.40% organic matter, typical values for the sandy roadbank habitats in which it is found. South of 60°N latitude, *P. proligera* rarely occurs in alpine tundra, but occasionally grows along the margins of relatively humus-rich, subalpine streams. Organic matter content of such habitats are generally in the 2.5-3.0% range (fig. 26). In Alaska and the Yukon, however, *P. proligera* more frequently occurs in alpine tundra, where it may be found on the sides of some kind of natural micro-relief, or more commonly on soil mounds produced by disturbance in which mineral soil is exposed. It rarely grows among undisturbed tundra vegetation as do *P. drummondii* and *P. tundrae*. Possibly, competitive interactions with these two species exclude *P. proligera* from tundra habitats in which it may physiologically be able to exist.

Along the pH gradient (fig. 26), *P. proligera* occurs over a broad range (4.30-7.58), but has the highest mean value of any species investigated (5.93). It is the only species whose central pH niche extends above 6.00, 30% of the populations occupying the range from 5.74 to 6.17 (Table 2). *Pohlia proligera* populations show a distribution along the pH gradient that is significantly different from every other propaguliferous species measured except *P. filum,* which also tends to occur on soils of high pH. *Pohlia proligera* is the only propaguliferous species which I have found actually growing on soil in the crevices of outcropping limestone, and it sometimes co-exists with such calciphilic species as *P. vexans, P. wahlenbergii, Meesia uliginosa* Hedw., and/or *Cratoneuron filicinum* (Hedw.) Spruce.

It can be seen from figure 27, that *P. proligera* is rather broadly adapted to both the pH and the organic matter content gradients. This is likely to be one reason why *P. proligera* is distributed so widely in North America (fig. 60).

P. camptotrachela: Along the Pacific coast, *P. camptotrachela* has been collected from sea level up to the alpine zone of the Sierra Nevada-Cascade ranges. It occurs on sandy, or often gravelly soil along roadsides, drainage ditches, stream margins or sometimes on low- or subalpine soil almost lacking in organic matter. It is absent from organic-rich tundra soil, where it is replaced by *P. tundrae* or *P. drummondii*. Along the organic matter gradient (fig. 28), *P. camptotrachela* shows a narrow, strongly defined region of high population frequency in 1.0-1.6% range, and a secondary, less distinct region of high frequency around 2.4-2.8%. Samples comprising these higher values are those from some of the most organic-rich tundra soils on which *P. camptotrachela* is found. The soil in such alpine situations are richer in organic matter than typical soils underlying *P. camptotrachela* populations, but not so rich as the tundra soils on which *P. drummondii* and/or *P. tundrae* grow, which almost always contain 2.6-3.2% organic matter. Most of the soil on which *P. camptotrachela* grows, even within the alpine zone, contains less than 1.6% organic matter. The central niche of *P. camptotrachela* along the organic matter gradient is in the range of 1.25-1.47%, and these values represent its most typical habitat in roadside ditches and similar locales. It is usually absent from the sandy, somewhat stabilized roadbanks on which *P. proligera* and *P. annotina* are frequent, occurring rather at the base of such roadbanks where frequent minor floods are effective in washing away most traces of organic matter. In Washington and British Columbia, it is not unusual to find *P. annotina* growing up on the sides of roadbanks with *P. camptotrachela* growing on the coarser, less organic, more compacted soil along the base, yet the two only infrequently grow intermixed. The distributions of the two species along the organic matter gradient are significantly different at the 0.001 level (Table 4), and *P. camptotrachela* differs significantly at the same level of confidence from every other species investigated except *P. filum*. *Pohlia camptotrachela* rarely occurs in roadbank habitats in the central Rocky Mountains (e.g. Colorado), where it has only been found on alpine soil above 10,000 feet, presumably being restricted to the higher elevation by moisture requirements in these continental mountains. Populations more to the north in Wyoming and Montana occur at progressively lower altitudes as the macro-climate becomes more moist.

Pohlia camptotrachela also shows a narrowly defined region of high population frequency along the pH gradient (fig. 28), with a peak at pH 5.4 to 5.5. Its niche width along this gradient (0.35) is the lowest of any species in terms of pH, and a full 30% of the populations (its central niche) fall within a range of 0.3 pH units (5.42-5.69). Obviously, *P. camptotrachela* is a sensitive indicator for soil pH.

It can be seen from figure 29, that *P. camptotrachela* is somewhat more variable, in terms of its realized niche, along the organic matter gradient than along the pH gradient. However, 50% of the populations (the middle envelope in fig. 29) occur over a narrow range of both gradients. This narrow ecological amplitude along these two gradients may be indicative of narrow ecological tolerances in general, and this may, in part, explain its limited geographic distribution in North America (fig. 56). It is impossible at present to know, however, whether this restricted ecological amplitude is the result of a narrow fundamental niche, or whether *P. camptotrachela* is competitively inferior and is excluded from some areas in which it is physiologically able to exist.

Discussion

Populations of *P. tundrae* were collected over most of this species' geographic range, and therefore these data are probably a good representation of its general ecology (it is only presently known from North America). Samples cover most of the North American range of *P. camptotrachela*, but this species also occurs in Europe. The remaining species for which quantitative data are presented occupy a considerable area in North America which was not sampled, and also occur on other continents, so it is unknown to what extent these data can be generalized to other portions of their worldwide ranges. It would be of great interest to compare analogous data from European populations, since they are likely to have been isolated from their North American counterparts since at least the

Cretaceous period.

Root (1967) defined an ecological guild as a group of species which utilize common resources in a similar manner, regardless of their taxonomic affinities. This group of *Pohlia* species certainly constitute an ecological guild, frequently co-existing in interspecific mixtures, although it can be seen that each behaves individualistically along the gradients measured.

Most species are fairly evenly distributed along the pH gradient, with only *P. camptotrachela* (fig. 28) showing a very narrowly defined region of high population frequency. On the other hand, the central niche (30% of the populations) of each species is limited to the narrow region from about pH 5.3 to pH 5.7 (Table 2), and from figures 18, 20, 22, 25, 27 and 29, it can be seen that a full 50% of the populations of each species occupy an only slightly broader range of soil pH. This is in agreement with the suggestion by Ochi (1959 b), that *Pohlia* species are good indicators of soil pH. All species in the present complex may be considered to be mildly acidiphilic, although the precise region along the pH gradient in which populations are found, varies from species to species (fig. 15, 30). *Pohlia annotina* most frequently grows on soil of the lowest pH, being common on soil of pH 4.6 to pH 6.0, but is decidedly less common on soils of higher pH. *Pohlia proligera* is at the opposite end of the gradient, occurring frequently on soils of pH 6.0 and above, and was collected on soils of pH as high as 7.58. I have collected this species a number of times in the soil-filled crevices of exposed limestone, a habitat in which *P. annotina* is unlikely to be found. The Wilcoxan sign-rank test indicates that the distribution of these two species along the pH gradient is significantly different at the 1% level (Table 4). The distribution of *P. proligera* along this gradient also differs significantly from *P. tundrae, P. camptotrachela,* and *P. drummondii*.

As can be seen from figures 15, 16, species of the propaguliferous complex are more readily differentiated from one another in terms of organic matter content of their substrate than on the basis of soil pH. As suggested above, the propaguliferous species occur primarily in three habitats. *Pohlia drummondii* and *P. tundrae* are characteristic of alpine tundra, *P. annotina, P. proligera* and *P. camptotrachela* on sandy roadbanks, and *P. filum* on sandy or gravelly stream outwash. Alpine tundra soils range from about 2.5 to 3.2% organic matter, roadbanks about 1.8 to 2.5%, and sandy outwash from 0.6 to 1.3%. *Pohlia drummondii* and *P. tundrae* frequently grow intermixed, and in the central Rocky Mountains and Sierra Nevada-Cascade Ranges, one species is rarely found in an area in which the other is absent. Quantitative measures are not significantly different for these two species along either gradient (Table 4). Likewise, *P. proligera* and *P. annotina,* which both occur in the roadbank habitat, have distributions along the organic matter gradient which broadly overlap (fig. 31), and are not significantly different (Table 4). *Pohlia camptotrachela* also occurs along roadsides in the Pacific states of the U.S., but this species typically grows on soils of lower organic matter than those of *P. annotina* or *P. proligera* (fig. 31), and its distribution along this gradient differs significantly from the latter species (Table 4). As discussed above, the lower organic matter values for *P. camptotrachela* appear to be because of its occurrence at the base of such roadbanks, where flowing water frequently washes away most traces of organic matter. The last species, *P. filum,* occurs almost exclusively on soils of very low organic matter content (fig. 31). Its distribution along this gradient differs significantly from all other species except *P. camptotrachela*. It is perhaps noteworthy that these two species, which might come into competitive contact in similar habitats, overlap only minimally in geographic distribution (fig. 35, 56).

Table 5 summarizes the ecological differences which I have been able to document between these propaguliferous species in relation to two environmental gradients. It can be seen that every species differs from every other species along at least one of the two gradients, with the exception of *P. drummondii* and *P. tundrae*.

In several cases, species-pairs in which the species are very similar morphologically (and presumably closely related), are at opposing ends along an ecological gradient. For example, *P. proligera* and *P. annotina* are quite similar morphologically, and some authors (e.g. Wilczek and Demaret 1970, Lewis and Smith 1978) have even considered them conspecific. However, the two are widely separated along the pH gradient, *P. proligera* having the highest mean soil pH, and *P. annotina* the lowest value of any of the species thus far investigated. The two rarely co-exist in mixtures, and in Alberta, where the Rocky Mountains are highly calcareous, *P. proligera* occurs sporadically but *P. annotina* is absent. Likewise, *P. drummondii* and *P. filum* have been variously treated by many authors of floristic works, with the latter species sometimes considered a variety of the former species (e.g. Lawton 1971). These two species are extremely different ecologically (and quite distinct morphologically), *P. filum* occupying a specialized and narrowly defined habitat characteristically low in organic matter content (fig. 31). They, like *P. proligera* and *P. annotina*, only very rarely grow intermixed. *Pohlia tundrae* was illustrated by Flowers (1973) as *P. annotina* var. *decipiens*, and the author obviously felt that they (*P. tundrae* and *P. annotina*) are similar enough morphologically to be considered conspecific. See under *P. tundrae* in the systematic section for a discussion of the morphological distinctions between *P. tundrae* and forms of *P. annotina* with long, narrow propagula. Ecologically, the two species are widely divergent, *P. tundrae* being a characteristic alpine plant, and *P. annotina* a lowland-montane species. The two differ significantly along the organic matter gradient, the tundra substrate of *P. tundrae* having a higher percent organic matter content than the typical substrates of *P. annotina* (fig. 31, Table 5). *Pohlia tundrae* is also similar morphologically to *P. proligera*, which it resembles in the strong sheen characteristic of its leaves when dry. These two species, however, are distinct along both the pH and the organic matter gradients (Table 5).

Van Valen (1965) presented data which suggest that levels of morphological variability are directly correlated with niche width in some bird species. He found that on islands where a particular species has broad feeding habits, the species was morphologically variable, as compared to mainland populations in which nonvariable morphology reflected narrower feeding habits. According to Van Valen, this relationship held true for several unrelated taxa. Among the propaguliferous Pohlias, there also seems to be a correlation between niche width, geographic distribution, and the level of morphological variability. *Pohlia annotina* and *P. camptotrachela* are two very closely related species, but the former is extremely variable morphologically while the latter is notably stenotypic (see fig. 59). Lewis (1976) grew numerous populations of both species and found that some of the interpopulational variability of *P. annotina* was retained when grown in culture, while populations of *P. camptotrachela* were consistently uniform, and Lewis concluded that *P. annotina* was the more genetically variable of the two. As can be seen by comparing resource utilization curves for the two species (fig. 30, 31), the morphologically variable *P. annotina* is considerably more tolerant of a broader range of edaphic conditions and does not have a high population frequency in any small area of the gradients. This greater ecological amplitude of *P. annotina* is also reflected in its broader geographic range in North America (fig. 52, 56). It is also interesting that of the two species, *P. annotina* is more weedy (i.e. more frequently occurring in disturbed habitats) than is *P. camptotrachela*. The broader ecological amplitude of *P. annotina* is probably a pre-adaption for the evolution of "weediness". Isoenzyme methods could be a useful approach for comparing more directly the levels of genetic variability in these two species.

Of the propaguliferous species investigated, *P. proligera* and *P. annotina* most frequently occur in man-made habitats, and figures 25 and 27 indicate that their resource utilization along both gradients are the most generalized.

Their commonness as compared to the other propaguliferous species is certainly a reflection of their generalized ecological distribution. Baker (1974) has stressed the importance of what he called the "general purpose genotype" in the evolution of weediness, and these ecological data seem to be in agreement with his concepts. It would be of interest, however, to discern whether the broad ecological amplitude of *P. proligera* and *P. annotina* is indeed the result of general purpose genotypes, or whether populations of these species consist of numerous, individually specialized phenotypes.

Within the propaguliferous complex, some relationship exists between the degree of differentiation of the propagula and the degree of weediness of the species. *Pohlia drummondii* and *P. filum*, which have single propagula, are found less frequently as weeds than are the species producing numerous, small propagula. *Pohlia filum* sometimes grows on roadbanks in Alaska, but this species is not a frequent roadside weed, probably because of its edaphic limitation to soils of a narrow range of organic matter content. *Pohlia drummondii* is considered, on the basis of morphological evidence, to be the most primitive extant species of this complex. Ecologically, *P. drummondii* is most frequent in North America on alpine tundra soil, while most other species of the complex occur more frequently in specialized or man-made habitats. It can be speculated that the ancestor of these propaguliferous species was an alpine plant, and that species characteristic of specialized habitats (e.g. *P. filum, P. camptotrachela*) and those able to colonize man-made habitats are ecologically derived.

As early as 1859, Darwin noted that competition between morphologically similar, phylogenetically related species is likely to be particularly acute, because of their overall biological similarity. Whether speciation occurs sympatrically or allopatrically, once two genetically isolated species occupy the same geographic range, competition could cause the extinction of the competitively inferior species. One way by which competition may be avoided is through the evolution of niche and/or habitat differences between species, and this may occur either while the species are sympatric or when they are allopatric.

Differentiation of the *P. filum* type from the primitive "*P. drummondii* level of evolution" seems to have taken the course of divergence into a less humus rich habitat, and this was probably accompanied by morphological adaptions to the habitat. When Bruch, Schimper and Gumbel (1839) described *Bryum ludwigii* var. *gracile (= P. filum)*, they interpreted the variety as a dry habitat modification of the species. The smaller, more erect leaves of both the stem and propagula of *P. filum* are probably modifications (from the *P. drummondii* type) which are adaptive in drier situations.

Pohlia proligera, *P. annotina*, *P. camptotrachela*, and *P. bulbifera* may be considered ecologically derived from an alpine ancestor. Competition between *P. proligera* and *P. annotina* is mostly avoided by niche differentiation along the pH gradient, and *P. camptotrachela* avoids competition with either species by inhabiting less organic rich sites within the same habitat. The fact that each species is ecologically differentiated from closely related congeners suggests that ecological evolution has played some part in their phylogenetic history.

TAXONOMIC TREATMENT

A morphologically based classification of these propaguliferous species in *Pohlia* was arrived at by means of herbarium studies, field experience and culture of living plants. An attempt was made to examine herbarium specimens representative of all geographic areas in North America in which these species are known or expected to occur. Herbaria from which specimens were examined are listed in Table 6. Approximately 1600 specimens were examined from these herbaria, and I have collected each species on numerous occasions in their natural habitats. Specimens of *P. proligera*, *P. drummondii* and *P. annotina* were most common in many herbaria, and at least 200 collections were examined for each of these species. Approximate number of specimens examined of the remaining species are as follows: *P. tundrae* 75, *P. bulbifera* 125, *P. filum* 150, *P. camptotrachela* 100, *P. andalusica* 100, *P. andrewsii* 60. These are in addition to specimens collected by myself, and the latter are presently deposited in ALTA, with duplicates of most numbers in my own herbarium.

Each species presently recognized has been grown in pure culture. Cultures were grown on agar containing Hatcher's nutrient medium (Hatcher 1965) in 8 cm. high glass petri dishes. Cultured populations were initiated by propagula from plants collected in the field, and were maintained in controlled environment facilities with a 16 hour photoperiod under flourescent light. Additional populations of each species were initiated from spores when the latter were available. *Pohlia tundrae, P. drummondii, P. proligera* and *P. annotina* were also maintained in a greenhouse in pots containing a mixture of one half standard potting soil and one half sand. Such populations of *P. proligera* were maintained for more than two years,and those of *P. tundrae, P. drummondii,* and *P. annotina* for a minimum of seven months. Replicates of these greenhouse populations were initiated from propagula and spores of each species.

As only a limited number of populations of each species were grown, no statistical comparison of cultured versus field populations was undertaken. Limited morphological data comparing *P. proligera* and *P. annotina* in culture is given in figure 55. It was found that the time investment necessary for growing enough populations of each species for statistical comparisons would have precluded the possibility of conducting an adequate herbarium, nomenclatural, and ecological study.

Selected species were compared quantitatively with respect to the morphology of their propagula as found in herbarium specimens (fig. 44, 51, 55, 59). Each point on a scatter diagram represents the mean value derived from measurements of two propagula from each of three stems in a population (= specimen). Additional sampling information is given in the legend accompanying scatter diagrams when necessary.

Dichotomous Key to Populations of the Propaguliferous Species of *Pohlia* in North America

1 Propagula arising singly in the leaf axils 2

1 Propagula arising (3)- many in the leaf axils 3

  2 Propagula oblong to cylindric (fig. 34), usually at least twice as long as wide; primordia green and conspicuous, scattered on the bulbiform body; stems and propagula red when moist, red or black when dry; leaves spreading and often carinate .... 1. *P. drummondii*

  2 Propagula sphaeroidal to oblong, often elliptic (fig. 37), usually less than twice as long as wide; primordia pale and inconspicuous, mostly restricted to the apex; stems green when moist, black when dry; propagula green (when young) or orange (when older) when moist, often black when dry; leaves erect, scarcely carinate .... 2. *P. filum*

3 Propagula sphaeroidal, hardly longer than wide 4

3 Propagula oblong, obconic, or ± elongate and vermicular 6

4 Primordia of all propagula broadly triangular-laminal, conspicuously concave and forming a dome over the apex (fig. 47).... 5. *P. bulbifera*

4 Primordia of some or all propagula short and peglike, often incurved over the apex but not forming a complete dome 5

5 Plants glossy when dry; propagula distinctly red-translucent .... 6. *P. andrewsii*

5 Plants dull when dry; propagula yellow-translucent, occasionally brown, but never red .... 8. *P. camptotrachela*

6 Primordia of at least some propagula short, peglike and incurved over the apex; propagula mostly less than 120 um long.... 6. *P. andrewsii*

6 Primordia on all propagula well developed, elongate and erect or bent at an angle from the propagulum body (cf. fig. 62: 16-18), never incurved over the apex; propagula greater than 150 um long 7

7 Leaf primordia distinctly laminal in form; plants glossy 8

7 Leaf primordia peglike, rarely becoming ± laminal on very large, bulbiform propagula (fig. 54); plants dull or glossy 9

8 Propagula linear-cylindric (fig. 43) .... 4. *P. tundrae*

8 Propagula obconic to oblong-bulbiform (fig. 40) .... 3. *P. andalusica*

9 Plants dull when dry; propagula with (2)-3-4-(5) peglike, erect primordia (occasionally becoming ± laminal on old propagula), obovate, obconic to elongate and narrowly turbinate or occasionally ± bulbiform, rarely vermicular, mostly greater than 80 um wide at the broadest point (fig. 54) .... 7. *P. annotina*

9 Plants glossy when dry; propagula with 1-2 peglike primordia, often (when single) bent at an angle to the propagulum body, linear vermicular, never bulbiform, mostly less than 60 um wide at the broadest point (fig. 62) .... 9. *P. proligera*

1. *Pohlia drummondii* (C. Mull.) Andr. *in* Grout, Moss Fl. N. Am. 2. 196. 1935.

Bryum drummondii C. Müll., Bot. Zeit. 20: 328. 1862. Type: Drummond, Musci Amer (Rocky Mtns.) no. 263 as *Bryum nutans* var. *minor* (Lectotype: BM-Hampe !; isotype: NY-Mitten !).

Webera drummondii (C. Müll.) Jaeg., Ber. S. Gall. Naturw. Ges. 1874-1875: 137. 1876.

Bryum catenulatum Schimper, Syn. ed. 2: 471. 1876. Type: "Ben Lomond, leg. J. Stirton" (Lectotype: BM-Schimper !).

Webera commutata Schimper, Syn. ed. 2: 403. 1876. Type: "in Vogesi super. m. Hoheneck ... (BM-Schimper !), in

Cebennis et Pyrenaeis ..., Grimsel ... (Lectotype: BM-Schimper!), in m. Albula ad Weissenstein ..., in m. Tatra ..., Tromso ...."

Pohlia commutata (Schimper) Lindb., Musci Scand. 17. 1879.

Bryum commutatum (Schimper) Boul., Muscin. France 1: 278. 1884.

Webera subcucullata C. Müll. & Kindb. *in* Macoun & Kindb., Cat. Canad. Pl. 6: 113. 1892. Type: "Mt. Queest, Gold Range, B.C., July 27th 1889, Macoun (S-Kindb. !) ... North of Griffin Lake, Gold Range, B.C., August 8th 1889, Macoun" (Lectotype: S-Kindb. !).

Webera pycno-decurrens C. Müll. & Kindb. *in* Macoun & Kindb., Cat. Canad. Pl. 6: 114. 1892. Type: "North of Griffin Lake, Gold Range, B.C., leg Macoun" (Lectotype: S-Kindb. !).

Webera micro-denticulata C. Müll. & Kindb. *in* Macoun & Kindb., Cat. Canad. Pl. 6: 114. 1892. Type: "North of Griffin Lake, Gold Range, B.C., July 27th 1889, Macoun ...." (Lectotype: S-Kindb. !).

Webera commutata var. *catenulata* (Schimper) Dixon, Stud. Handb. Brit. Moss. 309. 1896.

Bryum micro-commutatum Kindb., Bot. Not. 1896: 197. 1896. Type: "Norge, nära Kongsvold" (Lectotype: S-Kindb. !).

Bryum subpolymorphum Kindb., Eur. N. Am. Bryin. 2: 390. 1897. Type: "Alp. regions r. Amer. Can. Brit. Col. 1950 metr. a sea: Macoun Canad. musci n. 468" ("British Columbia, Gold Range, Macoun, 8.8.1889" Lectotype: S-Kindb. !).

Bryum microsporum Kindb., Eur. N. Am. Bryin. 2: 388. 1897. *nom. illeg. incl. spec. prior.*

Webera subpolymorpha (Kindb.) Paris, Index Bryol. 1360. 1898.

Webera micro-commutata (Kindb.) Paris, Index Bryol. 1354. 1898.

Bryum alpinum var. *denticulatum* Card. & Thér. *in* Holzinger, Bot. Gaz. 30: 123. 1900. Type: "Lake MacDonald, northwestern Montana, leg Holzinger & Blake" (Isotype: MIN ! BH !).

Pohlia subpolymorpha (Kindb.) Broth. *in* Engler & Prantl, Nat. Pfl. 1 (3): 548. 1903.

Pohlia lindbergii Warnst., Beih. Bot. Centralbl. 16: 240. 1904. Type: "Schweden: Dalarna Avesta, Lindnäs, im August 1881 leg. Conrad Indebelon (Herb. Lindberg)." (Lectotype: H-SOL !).

Pohlia commutata var. *lindbergii* (Warnst.) C. Jens. *in* Weim., Foert. Skand. Vaext. 2 (Moss): 36. 1937.

Webera commutata var. *lindbergii* (Warnst.) C. Jens., Skand. Bladmfl. 158. 1939.

Bryum jutunheimii Hagen *ex*Podp., Act. Ac. Sc. Nat. Morav. 17: 93. 1945. (*nom nud in synon.*).

Pohlia drummondii var. *catenulata* (Schimper) Podp., Consp. 338. 1954.

Pohlia drummondii var. *lindbergii* (Warnst.) Podp., Consp. 339. 1954.

Plants sometimes forming deep, extensive turfs in moist lowland or montane habitats, often dense and compact in alpine areas, ± glossy when dry; stems 3-15-(50) mm. high, distinctly red when moist (except at the apex), red or often black, at least near the base when dry, simple or occasionally once innovating at the base when sterile, simple or often once innovating below the perigonia when fertile; leaves erect to spreading, ± strongly carinate and sometimes somewhat flexuose when dry, when moist, ± spreading and sometimes carinate in elongate forms, more erect and concave in compact alpine plants, (0.55)-0.80-1.0-(1.80) mm. long, (0.20)-0.35-0.50-(0.80) mm. wide, lanceolate to ovate-lanceolate, acute, ± decurrent by 1-3 linear-rectangular cells, sometimes scarcely or not at all decurrent in compact expressions; margins plane, ± strongly toothed in the upper 1/3, entire to subentire below; costa ending 3-5-(6) cells below the apex, green in young leaves, green to red or rarely red-brown to black in older leaves; upper cells rectangular-rhombic to linear-rhombic, rarely ± vermicular, (35)-55-70-(95) um long, (6)-8-11-(14) um wide, undifferentiated at the margin or sometimes slightly narrower in a single row, rectangular near the base, 3-7:1; asexual propagula usually present in 1-3-(5) upper leaf axils of sterile shoots, sometimes few or lacking in compact, alpine forms, absent from fertile plants, arising singly in the leaf axils, generally uniform in appearance, shortly oblong when young, becoming ± elongate with age and state of development, ovate-oblong, bulbiform, mostly more than twice as long as wide, abruptly narrowed to a multiseriate stalk (which usually remains attached to the stem), (0)-400-600-(1500) um long, green when young, red when older, sometimes becoming black when dry, opaque, with (3)-4-6-(8), large, conspicuous, lanceolate, laminal leaf primordia scattered on the bulbiform body as well as at the propagulum apex, the leaf primordia mostly green and flexuose in appearance, arising as laminal appendages, never as peglike outgrowths; perigonia bulbiform, terminal on unbranched stems or the stems once (-twice) innovating below the perigonia; perigonial bracts abruptly acute to ± long and narrowly acuminate from an ovate, concave, ± red-brown base, ± strongly toothed near the apex; costa ending in the acumen; perichaetia terminal, inconspicuous; perichaetial bracts to 2.4 mm. long, narrowly lanceolate to ovate-lanceolate, often red at the base; costa ending in the apex or 1-3 cells below; median cells on average, longer and narrower than those of the vegetative leaves, 70-110 um long, 6-8 um wide, thin walled; margins revolute from above the base to just below the apex, toothed or rarely subentire in the upper 1/3. Dioicous; sporophytes rather frequent in compact, alpine populations having few asexual propagula; seta 1.0-2.0-(2.5) cm. long, orange-red to red; capsules positioned 100°-180°

from the vertical, 2.0-3.0 mm. long, shortly (to ± elongate) ovate-pyriform, with a well developed but short (to ± elongate) neck which becomes ± shrunken when dry; exothecial cells longitudinally elongate and ± rectangular to irregularly isodiametric, 30-55 um long, 15-28 um wide, with strongly sinuose walls, especially when dry, less so when moist, gradually smaller and less sinuose near the mouth, more nearly isodiametric and less sinuose in the neck, gradually elongate-rectangular just above the seta; stomata numerous in the neck, phaneropore, (25)-30-40-(45) um long; guard cells often with a red, ± conspicuous pigmentation in young capsules; annuli well developed, of 2-(3) rows of cells, remaining attached to the urn or the operculum, sometimes separating irregularly or very rarely ± revolvable; opercula conic and apiculate or rarely umbonate; exostome teeth 16, yellow-brown to brown above, often darker below, lanceolate, ± narrowly acute, coarsely papillose on the upper 1/3, more finely papillose below, endostome segments 16, hyaline, keeled and broadly perforate, cilia usually well developed, (0)-1-3 between the segments, long, ± nodulose, rarely short; spores clavate, (16)-18-21-(24) um; chromosome number N=11 (Ramsay 1969 - Vaucher not seen).

Nomenclature: During the 1820's, Thomas Drummond accompanied the Franklin expedition across Canada in search for a northwest passage to the Far East. Drummond collected bryophytes abundantly, later issuing the exsiccata set, *Musci americani* (Rocky Mtns.). No. 263 of the set had been collected on the "Summits of the Rocky Mountains, in wet places", and bore the label *Bryum nutans* var. *minor* Hook. Bruch and Schimper (in translation by Shuttleworth 1843) revised Drummond's exsiccati numbers, determining no. 263 A. as *Bryum (Pohlia) acuminatum* var. *pulchellum*, and 263 B. as *Bryum (Cladodium) arcticum.* The set which Bruch and Schimper annotated is presently located in Edinburgh (E) (Demaret & Wilczek 1978). Nearly twenty years later, Müller (1862 a) published the name *Bryum drummondii*, referring to Drummonds no. 263 as the type in his protologue. This resulted in a series of spirited exchanges between Schimper (1862) and Müller (1862 b), in which the former author reconfirmed the determinations made by himself and Bruch in 1843, while Müller reasserted that *B. drummondii* was indeed a new species (see pp.   for a detailed review of their discussions and also Demaret & Wilczek 1978). As might be guessed, Drummond's exsiccati of that number (263) was a mixed set, and the specimen studied by Müller was not the same as that revised by Bruch and Schimper (1843). Demaret and Wilczek (1978) succeeded in locating a specimen annotated by Müller in the British Museum (BM-Hampe !) and designated it as the lectotype of *Bryum drummondii*. Andrews (1935) examined an isotype from the Mitten herbarium in New York, and made the combination *Pohlia drummondii* (C. Müll.) Andrews, realizing that it was conspecific with the propaguliferous species referred to as *P. commutata* by earlier authors.

Bruch, Schimper and Gümbel (1839) published *Bryum ludwigii* var. *gracile* Schleich. *ex* B.S.G., and discussed its status as a dry habitat expression of the species. Wilson (1855) discussed the morphology of the variety in relation to *B. ludwigii*, saying that the var. *gracile* had not yet been found in Britain, and appeared to be restricted to the higher alps of Switzerland. However, he went on to comment (1855, p. 229) that "... an intermediate variety occurs near the summit of Ben Lawers, agreeing with the form assumed as the type of the species by Bruch and Schimper, and having the leaves somewhat carinate, less concave, more acute, and more erect and crowded than the form figured by Schwaegrichen, which is the same as that given in the supplement to *Eng. Bot.*" That same year, Wilson sent a letter to Bruch which is preserved at the British Museum (BM-Bruch). It discussed his opinion that *B. ludwigii sensu* Schwaegrichen was something other than the plant Bruch et al. (1839) had described under that name, and included small samples of *B. ludwigii* and the intermediate variety between that species and its variety *gracile* which he had spoken of. Apparently the recipient of the letter agreed with Wilson that the form was distinct from *B. ludwigii,* because in 1876, Schimper published the plant as *Webera commutata*. In his *Synopsis ...,* Schimper (1876) transferred the variety *gracile,* making the new combination *W. commutata* var. *gracile* (Schleicher *ex* B.S.G.) Schimper. Also in *Synopsis,* Schimper published *Bryum catenulatum* Schimper for an elongate, presumably wet habitat expression of the same species he described as *Webera commutata*.

During the 1890's, J.M. Macoun sent N.C. Kindberg a number of *Pohlia* specimens from the Selkirk Mountains of British Columbia, and over the period 1892 to 1897, Kindberg published four new species from two months of Macoun's collecting. I have examined type material for each (*W. subcucullata, W. pycno-decurrens, W. micro-denticulata* and *B. subpolymorphum*) from the Kindberg herbarium (S), and each falls easily within the morphological range of *P. drummondii*. An additional species, *Bryum micro-commutatum,* was described in 1896 from Norway, and this also falls within the range of variation of *P. drummondii*.

Demaret & Wilczek (1978) felt that the European *P. commutata* should be considered distinct from the North American *P. drummondii*. They distinguished the two species by differences in seta length, capsule position, operculum shape, exostome length, endostome morphology, and perigonial bract shape, and asserted that *P. drummondii* lacks propagula. While I also have been unable to locate propagula in any of the isotypes of *P. drummondii* (BM, NY), propaguliferous plants corresponding in every other respect to Drummond's no. 263 are frequent in North America. North American plants consistently produce propagula in culture, and rarely lack them in the field, although in herbarium specimens they are often difficult to find. The comment by Andrews (1935) that propagula are only occasionally produced by North American populations of *P. drummondii* was incorrect, and was probably because Andrews was more familiar with herbarium material of this species than populations in the field. *Pohlia drummondii* is far more common in western North America than in the east, where Andrews did most of his collecting. Peristome morphology, including exostome length, is a character showing some variation within species of the propaguliferous complex, as is seta length, operculum shape, and capsule position (see fig. 3: 9-11). Variation in perigonial bract morphology is discussed on pages 43-46. After having examined over 200 North American specimens of *P. drummondii*, and numerous European collections labelled *P. commutata* or *P. drummondii*, I cannot find any significant differences between specimens from the two continents, and therefore consider the two names synonymous.

Distribution: (fig. 32). Present collections of *P. drummondii* from North America indicate that this species is widely disjunct between stations in the western cordillera and those in the eastern portions of the continent. In the east, several collections are known from Baffin and Ellesmere Islands (the only confirmed reports from the arctic islands to date), and the species is scattered but infrequent south, to Massachusetts and New Hampshire in northeastern United States. Lesquereux was the first bryologist to collect *P. drummondii* in New England (White Mountains) and the three other records from eastern United States, two from New Hampshire and one from Massachusetts, were all collected by A.L. Andrews between 1910 and 1920 (BH !). It is noteworthy, that no more recent collections have come to my attention in spite of a rather extensive study of specimens from the eastern herbaria. With some additional searching along roadbanks and other montane to subalpine habitats, *P. drummondii* will most likely be found more frequently in the mountains of Vermont and New Hampshire. In spite of considerable collecting in the Adirondack Mountains of northern New York in recent years, *P. drummondii* has not yet been collected from that region and may be absent from the local flora (*P. andalusica* and *P. annotina* are frequent there). In western North America, *P. drummondii* is frequent in the central Rocky Mountains, and has been collected from Colorado northward to the province of Alberta. Andrews (1935) reported this species from Arizona, based on Bartram's collections and exsiccati, but the specimens (BH !, NY !, etc.) are not referrable to *P. drummondii*. They are puzzling forms (and as yet undetermined) with very elongate stems and more or less obtuse, cucullate leaves, and were collected from highly calcareous stream beds, sometimes submerged. They may be atypical expressions of *P. wahlenbergii*. Along the Pacific coast, *P. drummondii* has been collected from southern California northward to the southeastern panhandle of Alaska, mostly in the coastal mountains. In Alaska and the Yukon Territory, it is known from scattered localities northward to the north slope of the Brooks Range (Alaska) and eastward to the Hess Mountains (Yukon) and Logan Mountains (Northwest Territories). With additional collecting in north-central North America, *P. drummondii* may be found in intermediate regions connecting the eastern and western portions of its presently known disjunct distribution. On the other hand, *P. drummondi* is characteristically associated with mountainous regions, and its apparent discontinuous North American distribution may actually reflect its present occurrence. Non North American specimens have been examined from Austria, Czechoslovakia, East Germany, England, Finland, France, Greenland, Norway, Poland, Scotland, Sweden and Wales.

Selected Specimens Examined: Exsiccati. North America: Allen, Mosses of the Cascade Mtns. 55 as *B. commutatum* (CANM, H, MICH, MIN, WTU, UBC, US); Drummond, Musci Amer. (Rocky Mtns.) 263 as *B. nutans* var. *minor* (NY, BM); Grout, N. Am. Musci Perf. 459 as *P. drummondii* (NY, US, MICH, CAS, F, COLO, MIN, CANM); 462 as *P. gracilis* (MICH, UBC, F, US, MIN, CANM); Holzinger, Musci Acr. Bor. - Amer. 663 as *P. proligera* (COLO); Holzinger, Mosses of Northwestern Montana 49 as *W. commutata* (MIN); 50 as *W. carinata* (MIN); 51 as *W. carinata* (MIN); Sull. & Lesq. Musci Bor. Amer. (ed. 2) 265 as *B. cucullatum* (NYS - in part); 180 (ed. 1) as *B. annotinum* (BH - in part); 270 as *B. ludwigii* (MICH); Can.Musci 49 as *W. commutata* var. *microdenticulatum* (US); 62 as *W. commutata* (CANM); 326 as *W. commutata* (CANM); 408 as *W. commutata* (CANM); 423 as *W. commutata* (US, H, NY, WIS, CANM, MIN); 424 as *W. gracilis* (NY, WIS, MIN); 450 as *W. gracilis* (US, WTU, DUKE); 468 as *W. cucullata* (US); Macoun, Canad. Crypt. 47 as *W. nutans* var. *macrospora* (US); 50 as *W. pycno-decurrens* (US). *Europe:* Bauer, Musci Eur. Exs. 1092 as *P. commutata* (WTU, COLO); 1623 as *P. commutata* (ALTA, COLO, WTU - in part); Husnot, Musci Galliae 770 as *W. commutata* (BH, WIS); Lisowski, Bryoth. Polonica 287 as *P. commutata* (U); 732 as *P. commutata* (U). Canada. *Alberta:* Jasper Nat. P., Maligne Lake area, top of Bald Mtn., *Shaw 2847* (ALTA). Lake Louise, Macoun 179 (NYS). Above Peyto Lake, *Crum & Schofield 5167* (UBC). Kananaskis area, Fortress

Mtn. ski area, *Shaw 2830* (ALTA). Mtn. Park area, *Vitt & Peterson 6933* (ALTA). *British Columbia:* Cassiar Mtns., Stikine Range, *Vitt 19471* (ALTA). Revelstoke area, rd. up Mt. Revelstoke, *Shaw 2823* (ALTA). Nelson area, Kokanee Creek at Redfish cmgd., *Shaw 2767* (ALTA). Glacier Nat. P., along Lunch Creek just east of Logan Pass, *Shaw 2728* (ALTA). Nakusp area, 22 km. N of Nakusp on Hwy. 23, *Shaw 2212* (ALTA). Kicking Horse R. near Hector, *Brinkman 772* (BH). Okanagan Highland, Big White Mtn., *Eady,* 1968 (UBC). North Vancouver, Mt. Seymour, *Schofield 20104* (UBC). *Labrador:* Head of Kangalaksiorvik Fiord, *Weber 1527* (NFLD). Noodleook Fiord, *Weber 1490* (NFLD). Twin Falls area, Scott Falls, *Brassard 6397* (NFLD). *Northwest Territories:* Ellesmere Isl., head of Tanquary Fiord, *Brassard 3318a* (NFLD). Baffin Isl., Clyde R. *Polunin 2604-a-7* (UBC). Cumberland Sound, *Wynne-Edwards 33* (CANM). Logan Mtns., Lake close to Nahanni R., *Vitt 23285* (ALTA). *Prince Edward Island:* Queen Co., 2 mi. (1 mi. = 1.6 km.) S of Melville, *Ireland 13838* (CANM). *Quebec:* Ungava, vicinity of Helen Falls, *Weber 1348* (U). Rivieres Kogaluk et Payne, *Rousseau 696* (BH). Gaspe, Mt. Blanc, *Fabius 6145* (BH). *Yukon Territory:* Kluane P., *Scotter* 18223 (NY). 60 mi. S of Haines Jct., *Svihla 4007* (WTU). Bonnet Plume Range, Riparium Lake, *Vitt 16876* (ALTA). Selwyn Mtns., Itsi Range, *Vitt 22768,* (ALTA). Hess Mtns., Rogue Range, *Vitt 23557* (ALTA). U.S.A. *Alaska:* Juneau area, in front of

Mendenhall Glacier, *Shaw 1865* (ALTA). Skagway area, Upper Dewey Lake, *Shaw 2135* (ALTA). Amchitka Island, near Pond 29, *Reich 104* (CANM). Lake Noluk, 68°47'N, 160°W, *Spetzman M36* (US). *California:* Yosemite Nat. P., base of Mt. Dana, *Hall 64* (BH). Siskiyou Co., Squaw Valley Cr., *Koch 15756a* (UC). Inyo Co., Big Pine Lakes, *Howell,* 1947 (CAS). *Colorado:* Near Tolland, *Grout,* 1914 (DUKE). Jackson Co., 15 mi. SSW of Hebron, *Hermann 25716* (CANM). El Paso Co., Pikes Peak, *Richards & Rubinstein 1200* (F). Pitkin Co., ca. 5 mi. E of Aspen on Hwy. 82, *Shaw 2555* (ALTA). Gilpin Co., 20 km. W of Rollinsville on Corona Pass Road, *Shaw 2602* (ALTA). Larimer Co., 5 mi. W of Milner Pass on Hwy. 34, *Shaw 2673* (ALTA). *Idaho:* Elmore Co., Boise Nat. Forest, *MacFadden 19309* (UBC). Kootenai Co., Hope, *Sandberg 1206* (BH). *Montana:* Glacier Nat. P., Lunch Creek just E of Logan Pass, *Shaw 2728* (ALTA). Flathead Co., Lake McDonald, *Holzinger & Blake,* 1898 (MIN). *New Hampshire:* Randolf, *Andrews,* 1917 (BH). White Mtns., Kings Ravine, *Andrews,* 1918 (BH). White Mtns., *Lesquereux (sine no.)* (US). *Oregon:* Clackamas Co., Mt. Hood area, rd. to Sahalie Falls, *Shaw 2524* (ALTA). *Utah:* Salt Lake Co., Wasatch Mtns., *Flowers 4501* (COLO). Dushesne Co., Mirror Lake, *Flowers 4080* (COLO). Uintah Mtns., Ottoson Basin, *Flowers 9654* (COLO). *Washington:* Mt. Adams, Bird Lake, *Kozloff 31* (BH). Lewis Co., trail to Pinnacle Peak, *Lawton 50246* (WTU). King Co., Stevens Pass, *Sharp,* 1964 (WTU).

Snohomish Co., 0.25 mi. N of Barlow Pass on Mt. Loop Hwy., *Shaw 2335* (ALTA). Clallum Co., Obstruction Pk. area, *Shaw 2363* (ALTA). Pierce Co., Mt. Rainier, Paradise Pt., *Shaw 2402* (ALTA). *Wyoming:* Teton Co., banks of Bradley Lake Trail, *Shaw 2695* (ALTA). Albany Co., Little Brooklyn Lake, *Schrierer 21* (MICH). Park Co., Beartooth Lake, *Conard,* 1953 (CANM).

Pohlia drummondii is characterized by its 1) typical red pigmentation of the stem and older propagula 2) erect-spreading to wide-spreading leaves which generally become strongly carinate when dry and 3) the occurrence of 1-3 elongate, oblong, bulbiform, branchlike, axillary propagula which arise singly in the leaf axils and have conspicuous, flexuose, leaf primordia scattered on the bulbiform body as well as at the propagulum apex (e.g. cf. fig. 34: 6, 7). As a field character, the red pigmentation which is characteristic of the stem and "mature" propagula is the most reliable character to distinguish *P. drummondii* from other similar species. It should be noted, however, that the state of this character does vary to some extent, as do most taxonomic characters. When forming compact, alpine turfs, the stems of *P. drummondii* are often less distinctly red, the leaves are more erect and concave rather than carinate, and propagula are generally scarce. Such forms may appear vastly different than typical, elongate, montane or lowland expressions, but are related to the latter by a complete and continuous array of intermediate forms. Subalpine or low alpine individuals growing in slightly protected situations are more elongate than the typical, compact, alpine forms, and indicate that the latter (alpine) expression is nothing more than an extreme, phenotypic, habitat modification. Sporophyte production is quite frequent in these alpine populations, and is correlated with a relative scarcity of propagula in such forms. It was thought that perhaps this lack of propagula production is indicative of some genetic differentiation between montane (or lowland) and alpine expressions, but three populations of very compact, nonpropaguliferous, fertile, alpine plants produced abundant, typical, propagula when grown from either spores or propagula in a greenhouse at the University of Alberta. These compact modifications are accordingly considered phenotypic in nature, and are not given formal taxonomic recognition in the present work. Andrews (1935) reported that *P. drummondii* produces propagula only infrequently. Although they are often difficult to find in herbarium specimens, *P. drummondii* consistently produces 1-3 propagula in its upper leaf axils (except in the cases referred to above). Cultured populations have, in every case, produced abundant propagula. The propagula of *P. drummondii* vary in length with age and state of development, but otherwise are rather uniform in appearance. When very young in the upper most leaf axils (e.g. fig. 34: 1), the propagula are more or less isodiametric, pale to light-green, and have well developed, laminal leaf primordia which are very prominent relative to the size of the propagulum body. At this stage of development, they are not unlike young propagula of *P. filum* (e.g. fig. 37: 1), but the leaf primordia are even more prominent relative to the propagulum body, and in any case they are inconspicuous and rarely observed (unless searched for) in either species at this stage. When somewhat older (e.g. 3-5 leaf axils below the stem apex), the propagula of *P. drummondii* are still green, but are elongate-oblong, usually several times as long as wide, and have conspicuous, flexuose leaf primordia (e.g. fig. 34: 2-4). Later in the growing season, the propagula invariably become red, and I have observed little, if any, variation in "mature" color. The propagula of *P. drummondii* approach most closely, the presumed ancestral condition among this complex of propaguliferous Pohlias, and sometimes it is an arbitrary decision to distinguish them from deciduous branches. It is not uncommon to find branch-like structures lying loose in herbarium packets that represent propagula which have continued apical growth after falling from the stem (e.g. fig. 34: 8). Such structures have well developed central strands (fig. 34: 8) and the leaf "primordia" are actually costate. The only difference between these branch-like propagula and true axillary branches is that the propagula are separated from the stem by a constricted but multi-seriate stalk, in the region of which separation occurs. By sectioning propagula of varying lengths, it is possible to reconstruct the gradual, temporal differentiation of the central strand. The occurrence of these branch-like propagula is characteristic of *P. drummondii*, and I have not observed them in any other North American propaguliferous species except occasionally in *P. filum*. *Pohlia wahlenbergii* also occasionally produces deciduous branches that may be observed in herbarium packets (see also Nyholm 1958).

Alpine populations of *P. drummondii* which seem to lack propagula may be confused with *P. obtusifolia* or *P. bolanderi* when these are sterile. The taxonomic status of *P. bolanderi* will be discussed in detail in a future paper. The affinities of *P. bolanderi* are clearly with the *P. elongata-P. longicolla* complex, but when sterile it can appear rather similar to *P. drummondii*. *Pohlia bolanderi* is distinguished by its more or less erect, scarcely carinate leaves which have a distinctive blue-green metallic sheen, and by its lack of red pigmentation. When sporophytes are present, *P. bolanderi* differs in its elongate, narrowly pyriform, horizontal capsule, its readily revolvable annulus, and by its endostome segments which are only narrowly perforate. Both *P. bolanderi* and *P. drummondii* are dioicous, and have bulbiform, terminal perigonia. When sterile, *P. obtusifolia* can be distinguished from *P. drummondii* by its subtly, but definitely cucullate leaf apex, wider, laxer leaf cells (often to 15 um wide), and by its less distinct red pigmentation, although it is sometimes pink-stemmed. When sporophytes are present, *P. obtusifolia* is readily distinguished by its paroicous inflorescence, and by its slender, delicate, endostome segments (see Nyholm 1958).

The only other North American propaguliferous *Pohlia* with propagula arising singly in the leaf axils is *P. filum*. See under that species for the characteristics with which to distinguish it from *P. drummondii*. *Pohlia andalusica* can have propagula which are similar to those of *P. drummondii*, but they invariably arise in clusters in the former species (*P. andalusica*). When occurring in clusters, the obconic propagula of *P. andalusica* (e.g. fig. 40: 1-9) are distinct from any form of *P. drummondii* propagula. When larger, single propagula occur (e.g. fig. 40: 12-14), however, they can be confusingly similar to those of *P. drummondii*, but are distinguished by their red-brown color, their more rounded-oblong shape (e.g. compare fig. 40: 14 and 34: 7), and by the greater restriction of the leaf primordia closer to the propagulum apex. I should emphasize that the last character is most useful in conjunction with other characters, e.g. propagulum color and habit of the plants. In habit, *P. andalusica* differs from *P. drummondii* in its more slender stature, less strongly carinate, more erect leaves, and in its paler, often pink, but not red stem.

2. *Pohlia filum* (Schimper) Mårt., Svensk. Vet.-Ak. Arh. Natur. 14: 149. 1956.

Bryum gracile Schleicher, Cat. Pl. Helvet., ed. 4.39. 1821. *nom. nud.*

Bryum ludwigii var. *gracile* Schleicher *ex* B.S.G., Bryol. Europ. 4: 109. 1839 (fasc. 6-9. Mon. 39.). Type: specimen not cited. (Lectotype: BM-Schimper ! ["Bryum/Webera/ ludwigii var. β. Planta sterilis in foliorum axillis gemmifera. Grimsel, 25 August 1839"] ? leg. Schimper).

Bryum nivale Hooker *ex* Wilson, Bryol. Brit. 229. 1855. *(nom. nud. in syn.: B. ludwigii* var. *gracile).*

Webera ludwigii var. *gracile* (Schleicher *ex* B.S.G.) Schimper, Corall. 67. 1856.

Webera gracilis (Schleicher *ex* B.S.G.) De Not., Atti Univ. Genova 1: 418. 1869.

Bryum filum Schimper, Syn. ed. 2: 470. 1876. Type: "... prope Chamounix (Payot)." (Lectotype: BM-Schimper !).

Webera commutata var. *gracile* (Schleicher *ex* B.S.G.) Schimper, Syn. ed. 2: 404. 1876.

Pohlia gracilis (Schleicher *ex* B.S.G.) Lindb., Musci Scand. 17. 1879. *hom. illeg. (P. gracilis* Hornsch. 1819).

Webera ludwigii ssp. *gracilis* (Schleicher *ex* B.S.G.) Kindb.,

K. Svensk. Vet.-Ak. Handl., 7(9): 65. 1883.

Bryum commutatum var. *gracile* (Schleicher *ex* B.S.G.) Boul., Muscin. France 1: 278. 1884.

Bryum carinatum Boulay, Muscin. France 1: 280. 1884. Type: "Massif du Mt.-Blanc, sur plusieurs points, fert. vers le milieu de l'aiguille a' Bochard (Payot), Pelvoux près du lac. de l'Echauda (B[oulay])." (Lectotype: H-SOL ! [Mont-Blanc, chaînes des aiguilles Rouges, leg. Payot, determ. Boulay].

Webera cucullata var *carinata* (Boul.) Husn., Musci Gall. 229. 1889.

Webera carinata (Boul.) Limpr., Laubm. Deutschl. 2: 261. 1892.

Webera gracilis var *carinata* (Boul.) Amann, Rev. Bryol. 20: 43. 1893.

Webera commutata ssp. *gracilis* (Schleicher *ex* B.S.G.) Dix., Stud. Handb. Brit. Moss. 309. 1896.

Webera erecta A. Roth *ex* Corr., Unters. Vermehr. Laubm. Brutorg. 159. 1899. *hom. illeg.* Type: "Vom Schwarzwald, an der Strasse vom Ruhstein gegen Achern ... VIII 1896, VI und IX 1897."Type not seen.

Webera torrentium Hagen, Troms. Mus. Aarsh. 22: 110. 1899. Type: "No. Hatfjelddalen, Trollerud, Susenfjeldet, Löjpskaret 1300 m.: F.; Mo, Andfjeldet: A. (!); Bejeren, Tollåen: H.; Saltdalen, Ølfjeldet 500 m.: F.; Skjerstad, Balmifossen, beim Flusse Giken 520 m., nahe den "Ny

Sulitjelma" Gruben 570 m.: H. (Lectotype: TRH-*ex* herb. Hagen !). Tr. Bardo, Storfjeldet in der Weidenregion ♂; Nordrejsen, Javrreoaivve in der alpinen Region: A (!). F. Tanen, Algašvarre: Kaur. (!) (all specimens in TRH-Hagen).

Pohlia commutata var. *filum* (Schimper) Dus., Bih. K. Svensk. Vet. Ak. Handl. 27. Afd. 3 (1): 46. 1901.

Webera rothii Correns *in* Limpr. & Limpr. f., Laubm. Deutschl. 3: 728. 1902. (based on *Webera erecta* A. Roth *ex* Correns).

Pohlia torrentium (Hagen) Broth. *in* Engler & Prantl, Nat. Pfl. 1 (3): 549. 1903.

Pohlia carinata (Boul.) Broth. *in* Engler & Prantl, Nat. Pfl. 1 (3): 549. 1903.

Webera gracilis f. *elata* Loeske, Mossfl. Harzes 221. 1903. Type "bei Torfhaus und Oderbrück in chausseegräben (750-800 m.) ... Zwischen 1100 und 900 m. an der Ilsenburger Chaussee." (type not seen).

Pohlia rothii (Correns *in* Limpr. & Limpr. f.) Broth. *in* Engler & Prantl, Nat. Pfl. 1 (3): 551. 1903.

Webera commutata var. *filum* (Schimper) Loeske, Mossfl. Harzes 221. 1903.

Pohlia annotina var. *rothii* (Correns *in* Limpr. & Limpr. f.) Dism., Rev. Bryol. 32: 91. 1905.

Pohlia gracilis var. *elata* (Loeske) Loeske, Hedwigia 47: 181. 1908.

Pohlia carinata (Boul.) Loeske *in* Bauer, Hedwigia 48: 321.

1909.

Pohlia gracilis var. *torrentium* (Hagen) Arn. & C. Jens., Naturw. Unt. Sarekgeb. 3 (3): 1910.

Pohlia erecta (A. Roth *ex* Correns) Loeske, Herbarium 62: 132. 1922.

Webera annotina var. *erecta* (A. Roth *ex* Correns) Correns *ex* Dixon, Stud. Handb. Brit. Moss. ed. 3: 335. 1924.

Pohlia drummondii var. *gracilis* (Schleicher ex. B.S.G.) Podp., Act. Soc. Sci. Nat. Morav. Brno. 17 (4): 91. 1945.

Pohlia drummondii var. *filum* (Schimper) Podp., Consp. 338. 1954.

Pohlia drummondii var. *carinata* (Boul.) Podp., Consp. 338. 1954.

Pohlia schleicheri Crum, Bryologist 72: 244. 1969. (based on *Bryum ludwigii* var. *gracile* Schleicher *ex* B.S.G.).

Plants mostly slender, forming small scattered populations or occasionally extensive, dense turfs, ± glossy when dry, rarely dull, sometimes with the leaves ± 5-ranked and strongly carinate; stems 5-15-(60) mm. high, green above, green, orange, or sometimes red at the base when moist, black, at least near the base when dry, simple or once innovating at the base when sterile, simple or more often once innovating below the perigonia when fertile; leaves erect, imbricate to remote when dry, erect or occasionally ± spreading when moist; (0.5)-0.6-0.9-(1.5) mm. long, (0.2)-0.3-0.4-(0.5) mm. wide, narrowly to broadly lanceolate or sometimes ovate-lanceolate, abruptly acute, usually ± decurrent by 2-5 rectangular to rectangular-rhombic cells, sometimes scarcely or not at all decurrent in compact forms; margins plane, subentire to ± strongly toothed in the upper 1/3-2/3, subentire to entire below; costa ending 2-4-(6) cells below the apex, green in young leaves, green to red-brown or more often black in older leaves; upper cells rectangular to rectangular-rhombic, rarely vermicular, (35)-50-70-(85) um long, (6)-7-11-(14) um wide, thin-walled, undifferentiated at the margin, rectangular near the base, 2-6:1; asexual propagula usually present in 1-3-(5) upper leaf axils of sterile shoots, often scarce or absent in compact, alpine forms, absent from fertile plants, arising singly in the leaf axils, very rarely 2 per axil, rather uniform in shape, oblong or elliptic to subglobose, most often less than twice as long as wide, abruptly narrowed to a multiseriate stalk (usually remaining attached to the stem), (0)-300-600-(800) um long, green when young, orange to orange-brown when older, often becoming black when dry, opaque, with (2)-3-6 short, triangular-laminal leaf primordia present near the apex or sometimes lower on the bulbiform body, the leaf primordia inconspicuous, stiff and nonflexuose in appearance, arising as laminal appendages, never as peglike outgrowths; perigonia bulbiform, terminal on unbranched stems or frequently the stems once innovating just below the perigonia, lower leaves of perigonial plants often erect and ± strongly imbricate-appressed, causing the terminal perigonia to appear conspicuous; perigonial bracts abruptly acute from an ovate, concave, often red-brown base, entire to subentire or sometimes ± strongly toothed near the apex; costa ending 1-3 cells below the apex, in the apex, or occasionally excurrent as a short mucro; perichaetia terminal, inconspicuous; perichaetial bracts to ca. 2.5 mm. long, lanceolate to linear-lanceolate, often red at the base; costa ending in the apex or 1-5 cells below; median cells on average, somewhat longer than those of the vegetative leaves, linear-rhombic to ± rectangular, sometimes ± incrassate, to 100-(110) um long; margins revolute from above the base to just below the apex, subentire to ± toothed in the upper 1/3. Dioicous; sporophytes rather frequent; seta 1.5-3.0 cm. long, orange- to orange-red; capsules positioned 95°-145° from the vertical, 1.5-3.0 mm. long, short- to (rarely) ± elongate-pyriform, with a short- to (rarely) ± long neck which is often shrunken when dry; exothecial cells longitudinally-elongate and rectangular to irregularly isodiametric, 25-50 um long, 13-25 um wide, with strongly sinuose walls, especially when dry, less so when moist, gradually to abruptly smaller, less sinuose and sometimes thicker walled at the mouth, less sinuose and more nearly isodiametric in the neck, gradually to ± abruptly elongate-rectangular and thick-walled just above the seta; stomata numerous in the neck, phaneropore, (27)-30-38-(42) um long; annuli well developed, of 2-(3) rows of cells, remaining attached to the urn or the operculum, sometimes separating irregularly or rarely ± revolvable; opercula convex to conic and usually apiculate; exostome teeth 16, yellow to yellow-brown above, sometimes darker below, lanceolate, ± narrowly acute, coarsely papillose in the upper 1/3, more finely papillose below; endostome segments 16, hyaline, keeled and broadly perforate, rarely delicate and narrow above; cilia (0)-1-2-(3) between the segments, short or sometimes long and ± nodulose; spores baculate to clavate, (14)-16-19-(21) um.

Nomenclature: Because the propagula of *P. filum* are both conspicuous and distinctive, this species was probably one of the first propaguliferous species to be collected and studied by early bryologists. Leers (1775) was the first author to describe the propagula of any member of this complex, and Leers probably included *P. filum* in his concept of the propaguliferous species, *Mnium annotinum* (Leers 1775). See the section on nomenclatural history for a discussion of Leer's (1775) protologue, and later opinions as to the identity of his *Mnium annotinum*.

Roth (1794, 1800) and Hoffmann (1795) used the name *Trentepohlia erecta* for a propaguliferous taxon, and their concepts were probably composite ones including several species presently thought to be distinct. Roth (1794, 1800) did not illustrate *T. erecta* but Hoffmann's (1795) illustration (plate 14) shows a simple stem with erect leaves and a single, globose propagulum which clearly depicts the habit of *P. filum*. On-the-other-hand, a specimen labelled "*Trentepohlia erecta* Hoffmann, *ipse* Hoffmann" in the Hedwig-Schwaegrichen herbarium (G!) is *P. annotina*, and Hoffmann appears not to have distinguished these species. In 1800, Roth reported that his *Trentepohlia erecta* (1794) was nothing more than sterile plants of *Bryum annotinum* Hedwig.

Although Hedwig (1801) clearly illustrated *B. annotinum* (plate 43), one of his two herbarium sheets of this species includes nonpropaguliferous perigonial plants of *P. filum* (see under *P. annotina* and also Loeske 1905). These plants were distinguished on his herbarium sheet (no. 9-13 on the sheet marked "Olim Chemnitzii sax. lectum") as the variety *nivalis* Hook. *(in scheda)*, but no mention was made of this variety in the *Species Muscorum* .... The annotation must have been added after Hedwig's death. According to Wilson (1855 p. 229), Hedwig sent Turner a specimen of *P. filum* labelled *Bryum turbonatum*. Hedwig, like most authors before him (e.g. Leers 1775, Roth 1800), probably used the name *B. annotinum* in an inclusive sense, including *P. filum* as presently known, a fact which does not have bearing on his typification of *Bryum annotinum* Hedw.

Schleicher (1821) published the name *Bryum gracile* for the present taxon, but provided no description. There is a specimen in the Hedwig-Schwaegrichen herbarium (G !) bearing the notation, "*Bryum gracile* Schleicher", which is *P. filum*. Bridel (1827) likewise published *Bryum graçile* as a *nomen nudum*. Bruch, Schimper & Gumbel (1839) provided the first valid publication of a name for this species; *Bryum ludwigii* var. *gracile* Schleicher *ex* B.S.G. The plant was given specific status by De Notaris (1869 - as *Webera gracilis*), and Lindberg (1879) made the combination *Pohlia gracilis*. However, *P. gracilis* (Schleicher *ex* B.S.G.) Lindb. (1879) is a later homonym of *P. gracilis* Hornsch. (1819) (= *P. minor* Schwaegr., fide Index Muscorum) and is therefore illegitimate. The next available name is *Bryum filum* Schimper (1876), and Mårtensson (1956) made the combination in *Pohlia*, as was noted by Lewis & Smith (1978). Although Mårtensson's combination is presently accepted, it has been pointed out (Isoviita in litt.) that there might be considered sufficient reason to reject it as invalid, as article 33 of the ICBN requires a direct reference to the basionym when publishing a new combination. Mårtensson's combination, *P. filum* (Schimper) Mart. was made in part II of his work, while the complete reference to Schimpers' publication was provided in the bibliography which appeared in part III. The two parts of Mårtensson's thesis were possibly distributed a few days apart, and it could be argued that this invalidates the combination. This is, however, a question of hairsplitting (as was also pointed out by Isoviita), and I consider it best to accept Mårtensson's combination, especially because he did refer to the page (p. 270) of Schimper's *Synopsis Muscorum Europaeorum* at the time he proposed his new combination (part II, p. 149). Other authors (e.g. Brotherus 1903) have made no more direct reference than this when publishing new combinations.

Several other species are here considered synonymous with *P. filum* for the first time, and consequently some explanation is probably appropriate. Boulay (1884) described *Bryum carinatum* from Mont Blanc in southeastern France, making no mention of axillary propagula in his protologue. Limpricht (1892) made the combination *Webera carinata* (Boul.) Limpr., and Brotherus (1903) transferred this species to the genus *Pohlia*. Cardot and Thériot (1900) reported *Webera carinata* from North America based on a specimen collected in Montana by J.M. Holzinger and J.B. Blake (in 1898), but the specimen (MIN: *ex* herb Holzinger !) is *Pohlia drummondii*. European bryologists have used the name *Bryum (Pohlia,* etc.*) carinatum* with varying applications. Loeske (1909) discussed the species at some length, saying that northern bryologists had been using the name for elongate forms of *P. obtusifolia* (as *P. cucullata*), while many other European bryologists applied it to compact, carinate, convergent forms of *P. drummondii* (as *P. commutata*), *P. obtusifolia* (as *P. cucullata*), *P. andalusica* (as *P. rothii*) and/or *P. filum* (as *P. gracilis*). Nyholm (1958) stated that Scandinavian collections of *Bryum carinatum* are a form of *P. drummondii*. In his protologue, Boulay (1884) referred to two specimens, one collected by himself (Pelvoux (Dép. Hautes-Antes) près du lac de l'Echauda.) and the other collected by V. Payot (Aiguille à Bochard, Massif du Mont-Blanc, Dep. Haute-Savoie). Neither syntype could be located in Boulay's herbarium in LILLE, although a scrap of paper bearing a manuscript description by the hand of Boulay was found (!) (R. Lericq, in litt.). An effort was made to locate isosyntypes at CGE, G, MANCH, MPU and PC with no success, but one specimen evidently named by Boulay was found in H-SOL. The specimen ("Mont-Blanc, Chaînes des aiguilles Rouges, leg. Payot, determ. Boulay") is a compact form of *P. filum* with erect, imbricate, strongly carinate leaves, and with a few typical *P. filum* propagula loose in the packet. Apparently, Boulay overlooked the propagula when describing his new species. According to Hagen (1899), Payot distributed three different species as *Bryum carinatum*. I have examined two other specimens (besides the one in H-SOL) labelled *B. carinatum*

Boulay from the herbarium of N.C. Kindberg (S). One specimen (Husnot, *Musci Galliae* no. 772), collected by Payot (En montant au Brévent (Savoie)), I interpret as an elongate expression of *P. obtusifolia*. Sporophytes and gametangia are absent, but the leaf cells are lax (often greater than 15 um wide), and the leaves are slightly cucullate. The other specimen (Flora Helvetiae et Sabaudiae no. 59) was collected by Payot and H. Bernet and bears the locality description "Chanonii-Aiguilles Rouges." It is very similar to the previous specimen, and I interpret it also as *P. obtusifolia*. Of these specimens, only the once cited above from H-SOL could be considered an isosyntype of *B. carinatum*, and it is consistent with Boulay's protologue in every respect. Consequently, in the absence of a specimen from the Boulay herbarium, the one in H-SOL is suggested as *lectotypus nova*. It should be added that although *Bryum carinatum* Boulay (1884) was predated by *B. carinatum* Bridel (1827), the latter name was published as a *nomen nudum* in synonymy of *B. cucullatum*, and need not therefore be considered nomenclaturally.

Hagen (1899) compared the description of *Webera payotii* (Schimper) Limpr. given by Limpricht (1892) with that given in the original protologue by Schimper (1876), and concluded that these authors were applying the same name to different plants. He (1899) consequently felt that Limpricht's plant was without a name, and proposed *Webera* *torrentium* for the "neglected" species. In his discussion, Hagen (1899) reviewed the features distinguishing *W. torrentium* from *Webera carinata* and *P. drummondii* (as *W. commutata*), but did not mention *P. filum* (nor as *P. gracilis*). He did not consider the propagula, but distinguished these three species by differences in the morphology of their perigonial bracts. An examination of 12 specimens, including four syntypes, named *W. torrentium* (or *W. payotii* Limpr. (sic)) by Hagen revealed that Hagen was applying the name to elongate expressions of *P. filum*. Typical propagula (e.g. cf. fig. 37: 3, 4) were present in most specimens.

Pohlia rothii is presently considered a synonym of *P. filum*, the reasons for which are given under *P. andalusica*. North American bryologists have frequently applied the name *P. rothii* to *P. filum* because the illustration given by Andrews (1935) showed this species (it was reproduced from Correns' 1899 plate for *Webera erecta*).

Distribution: (Fig. 35). *Pohlia filum* has been collected from scattered localities across low and subarctic North America. It has not been collected in the Rocky Mountains south of Alberta, but is found in Washington and Oregon in the coast ranges. In eastern North America it has been collected from Baffin Island and the Keewatin in the North, to Gaspe and Prince Edward Island in the south. There are scattered localities across North-central Canada and undoubtedly the species is more common than collections would presently indicate from areas such as continental Northwest Territories and northernmost Ontario, Manitoba and Saskatchewan. In western North America, there are a number of collections from Alaska ranging from the North slope of the Brooks Range (Noluck Lake) to the Kenai peninsula and the state's southeastern panhandle. *Pohlia filum* is notably frequent and well developed along the Pacific Coast of Alaska and northern British Columbia, as indicated both by herbarium collections and personal observation. Additional collections have been seen from the Aleutian Islands to Attu Island, the westernmost of the chain. Most probably, *P. filum* ranges continuously across to, and along the Pacific rim of northwestern Asia. In British Columbia, *P. filum* occurs occasionally in the interior Selkirk Mountains, and extends southward along the Cascade Mountains to Crater Lake, Oregon. This species has been collected by numerous bryologists at Mt. Hood, Oregon, at least since T.C. Frye collected it in 1921 (WTU !). Except for the Crater Lake locality, Mt. Hood is the southernmost station for *P. filum* in North America. Non North American collections have been examined from Austria, Czechoslovakia, Denmark, East Germany, Federal Republic of Germany, Finland, Greenland, Iceland, Italy, Norway, Poland, Scotland, Sweden and Switzerland.

Selected Specimens Examined: Exsiccati. North America: Macoun, Can. Musci 76 as *W. annotina* (CANM); 162 as *W. annotina* (MIN); Europe: Bauer, Musci Eur. Exs. 313 as *P. gracilis* (F, BH); 314 as *P. gracilis* (F, BH); 315 as *P. gracilis* (F, BH); 905 as *P. gracilis* (F, WTU); 906 as *P. gracilis* (F, WTU); 1094 (WTU, F - in part); 1388 as *P. gracilis* f. *elata* (WTU, F. CANM); Bauer, Bryoth. Bohemica 124 as *W. commutata* var. *filum* (WTU); Brotherus, Bryoth. Fenn. 337 as *P. bulbifera* (US); Cryptogamae Exs. 4098 as *W. annotina* (MO, US, COLO); Kopsch, Bryoth. Saxonica 51 as *P. gracilis* (U); Lisowski, Bryoth. Polonica 458 as *P. rothii* (CANM). Canada. *Alberta:* Jasper Nat. Park, Mt. Edith Cavell, *Vitt 11799* (ALTA). *British Columbia:* Prince Rupert area, along Oldfield Cr. in Prince Rupert, *Shaw 1562* (ALTA). Revelstoke area, ca. 10 mi. (1 mi. = 1.6 km) S of Revelstoke at Blanket Cr. Cmgd., *Shaw 2196* (ALTA). Kokanee Glacier Prov. P., Esmerelda Creek Trail, *Shaw 2769* (ALTA). Mi. 75 of Haines Hwy., *Crum & Schofield 9617* (CANM). Stickine Glacier, *Cooper*, 1916 (DUKE). *Labrador:* Head of Kangalaksiorvile Fiord, *Weber 1519* (NFLD). Tasiuyak arm of Nachvak Fiord, *Weber 1617* (NFLD). Churchhill Falls, *Brassard 5513* (NFLD). *Northwest Territories:* Great Bear Lake, head of Hornby Bay, *Steere 10500* (NY). Baffin Island, Coronation Fiord, *Blouin 1079* (CANM). Head of Clyde Inlet, *Wynne-Edwards 9300a* (NY). *Prince Edward Island:* Prince Co., 5 mi. east of Richmond,

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Ireland 10318 (CANM). *Quebec:* E. coast of Hudson Bay, Great Whale River, *Marr M412* (NY). E bank of George R., 57°60'N, 65°33'W, *Weber 1320* (NFLD). *Saskatchewan:* Lake Athabasca, *Hermesh M2* (ALTA). *Yukon:* Lake Lindeman, *Williams,* 1898 (US). Klondike River Bank, *Williams,* 1899 (NY). Kluane Nat. Park, *Scotter 20344* (NY). Selwyn Mtns., Itsi Range, *Vitt 23195* (ALTA). Hess Mtns., Keel Pk. area, *Horton 5628* (ALTA). Between Mt. Archibald & Mt. De Coeli, *Crum & Schofield 9082* (CANM). U.S.A. *Alaska:* Kenai peninsula, Portage Glacier, *Vitt 18533* (ALTA). Circle Quad., vicinity of Eagle Summit, *Steere 72-819* (NY). Icy Bay, *Mazaika,* 1946 (MICH). De Long Mtns., Noluck Lake, *Steere 63353* (NY). Healy Quadrangle, 2 mi. E of Cantwell, *Hermann 21275* (DUKE). 15 mi. E of Ferry, *Benninghoff,* 1948 (NY). Juneau area, in front of Mendenhall Glacier, *Shaw 1860* (ALTA). *Mehner,* 1904 (WTU). Ketchikan area, ca. 5 mi. N of Ketchikan at Ward Lake Cmgd., *Shaw 1668* (ALTA). Skagway area, around Upper Dewey Lake, *Shaw 2126* (ALTA).

In the field, *P. filum* is a very distinctive species, characterized by its 1) ecological setting on very inorganic, sandy, mostly exposed substrates, 2) plants slender, with the leaves imbricate to remote but usually erect, and 3) its globose to oblong or elliptic, bulbiform propagula which arise singly (very rarely 2) in a few upper leaf axils. When well developed, in a sunny but frequently moistened habitat, *P. filum* forms extensive turfs of erect, sterile, stems, often 1.5 to 3.0 - (6.5 !) cm. high, with abundant, green propagula present on most stems. Frequently, patches of male plants, and female plants with sporophytes are also present within well developed turfs. When growing in unusually shaded habitats, the leaves of *P. filum* may be more lax and spreading, but such situations are unusual. The plants may be paler, lack or scarcely have the sheen typical of its leaves in sunny habitats, and the leaves are often larger and sometimes more broadly ovate-lanceolate (e.g. fig. 36: 1). Also in such habitats, the propagula may have leaf primordia which are larger, laxer, and more flexuose, green and conspicuous. In very exposed, rather arid situations (e.g. Mt. Hood, Oregon, or Mont Blanc, France - cf. the type of *Bryum carinatum* Boul.), *P. filum* may be very compact, barely 5 mm. high, and have erect, imbricate, smaller leaves (fig. 36: 7-9). Sometimes such forms have the leaves more or less distinctly 5-ranked and strongly carinate. These compact, xeromorphic expressions often have few propagula, and the leaf primordia are mostly small, triangular, and restricted to the apex. For the most part, the propagula of *P. filum* are very uniform in shape; when young, they are globose, pale green, and the primordia are well developed in relation to the size of the propagulum body (fig. 37: 1). Older propagula vary from sub-sphaeroidal to oblong or elliptic, but are rarely elongate and branchlike. They are still green when well developed and conspicuous in early summer, usually become more or less orange during the course of a growing season, and characteristically (but not always) become almost black when dried. The leaf primordia arise as laminal appendages (fig. 37: 1, 11: 3), and are often restricted to the apical region of larger propagula. This is not always the case, however, and sometimes a few scattered, stiff-looking primordia are present as far as midway down the bulbiform body (e.g. fig. 37: 5, 6). As noted above, when growing in atypically shaded situations, the propagula of *P. filum* may have larger, more conspicuous, sometimes flexuose leaf primordia. Such forms can be distinctly convergent with, and difficult to distinguish from *P. drummondii* (see also below).

Pohlia filum and *P. drummondii* are the only two North American propaguliferous Pohlias which have propagula that actually arise singly in the leaf axils. Sometimes *P. filum* and *P. drummondii* can appear very similar, especially as herbarium specimens, but the two species seem to actually intergrade very little, if at all (Loeske made the same observation on several occasions, e.g. 1907, 1922). When both are in their typical states, *P. drummondii* can be distinguished from *P. filum* by its larger, more spreadihg leaves that are more strongly carinate when dry, the characteristic red pigmentation of its stem and propagula when living, and by its elongate-oblong, clearly branchlike propagula with conspicuous, flexuose, scattered leaf primordia (e.g. fig. 34). The propagula of *P. drummondii* are green when young, even when they reach a conspicuous size, but consistently become red later in the growing season. Some authors have distinguished these two species on the basis of the relative restriction of the leaf primordia to the propagulum apex in *P. filum*, as opposed to their more scattered occurrence on propagula of *P. drummondii*. While it can be seen that this is generally true from comparing figures 11: 4 and 34 with 11: 5 and 37, it is also clear from fig. 37: 5, 6 that the primordia of *P. filum* propagula may also occur lower on the bulbiform body. When determining specimens, it is the smaller size, triangular shape, and stiffer appearance of the primordia that is most reliable in distinguishing *P. filum* from *P. drummondii* (fig. 34, 37). Propagula on *P. filum* plants growing in atypically shaded situations do sometimes have conspicuous, well developed primordia, and such plants can be difficult or impossible to distinguish from *P. drummondii*.

Among the species with clustered propagula, *P. filum* might only be confused with *P. andalusica*, when this latter species has only a few, large propagula present, and with much rarer forms of *P. annotina* which may likewise have only a few, bulbiform propagula. *Pohlia filum* and *P. andalusica* have been frequently confused in the past (see pages 98-101). When *P. andalusica* has clusters of obconic propagula in its leaf axils (fig. 5: 5), there is no confusing this with *P. filum*. However, when some compact forms of *P. andalusica* have only one to a few, bulbiform propagula present (e.g. fig. 5: 5, lower leaf axils), the plants often have erect, more or less imbricate leaves. In the field, there are usually at least a few propagula present, indicating that they had arisen in clusters, but sometimes herbarium specimens may appear to have single propagula. These can be problematic, but most often it is possible to find some of the typical, obconic propagula (fig. 40: 1-9) present free in the herbarium packet if it is *P. andalusica* (see also under that species). The propagula of *P. filum* (e.g. fig. 37: 2-4) can be distinguished from the oblong-bulbiform propagula of *P. andalusica* (e.g. fig. 40: 12-14, 11: 5) by their distinct constriction at the apical region from whence the primordia arise, giving them an egg-shaped appearance, and by their green to orange color which contrasts the typical red-brown of *P. andalusica* propagula.

Occasionally, specimens of *P. annotina* have only one to a few large, (e.g. 350 um long), bulbiform propagula (fig. 54: 23-26) present in scattered leaf axils. See under *P. annotina* for a discussion of these forms. They may appear similar to plants of *P. filum* but can be distinguished by the following points. 1) The plants have spreading to wide-spreading leaves which lack any conspicuous sheen when dry. 2) The perigonial plants, when present (they are not rare), have perigonial bracts with a long, and narrowly attenuate acumen. 3) The propagula are distinctly translucent, and the leaf primordia are gradually differentiated from the bulbiform body (e.g. fig. 54: 26) and this is made conspicuous by the similarity in color and translucent quality of both body and primordia. 4) The propagula are usually present in several leaf axils down the stem, and are gradually large toward the ground. The propagula of *P. filum* attain their "mature" size rapidly when only a few leaves below the apex of the shoot (fig. 37: 7), and do not display this gradual increase in size toward the base. Those forms of *P. annotina* with very large, bulbiform propagula have only been observed in European specimens and are rare or absent in North America (see under *P. annotina*).

3. *Pohlia andalusica* (Höhnel) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 551. 1903.

Webera andalusica Höhnel, Sitz. Ak. Wiss. Wien Math. Nat. Kl.Abt. 1. 104: 326. 1895. Type: "... am 28 September 1892 in circa 2800 M. hohe an feuchten Orten sudwestlich vom Picacho de Veleta in der Sierra Nevada ... leg. & det. Höhnel" (Lectotype: FH-Schiffner !).

Webera annotina var. *glareola* Ruthe & Grebe *in* Grebe, Hedwigia 40 (Beibl.): 109. 1901. "... auf den Steinschutthalden der Alten Kupferbergwerke bei Marsberg in Westfalen ... bereits 1893 (!) ... Juni 1897 (!) und 1898 (Lectotype: KASSEL-Grebe !).

Webera glareola (Ruthe & Grebe *in* Grebe) Limpr. *in* Limpr. & Limpr. f., Laubm. Deutsch. 3: 726. 1902.

Pohlia glareola (Ruthe & Grebe *in* Grebe) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 550. 1903.

Pohlia annotina var. *glareola* (Ruthe & Grebe *in* Grebe) Warnst., Krypt. Fl. Brandenburg 2: 429. 1904.

Pohlia rothii var. *compacta* Ruthe & Loeske *in* Loeske, Verh. Bot. Ver. Brandenburg 46: 162. 1905. Type: "vom Harzburg ... auf der stecke bis Torfhaus ... und Konigskrug ...." (Lectotype:B-Loeske !).

Pohlia hercynica Warnst. *in* Bauer, Oest. Bot. Zeit. 63: 106. 1913. Type: Bauer, Musci Eur. Exs. Ser. 19. No. 907 a & b (Lectotype:B-Warnst !).

Pohlia grandiflora var. *glareola* (Ruthe & Grebe *in* Grebe) Podp., Consp. 340. 1954.

Pohlia camptotrachela var. *glareola* (Ruthe & Grebe *in* Grebe) Wijk & Marg., Taxon 14: 197. 1965.

Plants generally forming small, pure populations, sometimes in extensive turfs or occasionally intermixed with other mosses, lax forms with a distinct gloss, often more dull when small and compact, sometimes appearing 5-ranked with the leaves strongly carinate; stems 2-15-(30) mm. high, green above, often ± red or sometimes black below, simple or sometimes once innovating near the base when sterile, simple or often innovating below the perigonia (or occasionally the perichaetia) when fertile; leaves erect to ± spreading when dry, spreading to ± erect when moist, (0.50)-0.70-0.90-(1.10) mm. long, 0.20-0.40-(0.50) mm. wide, narrowly to broadly lanceolate, abruptly to ± gradually acute, shortly and narrowly decurrent by 1-3 rectangular-rhombic cells, sometimes nondecurrent on compact forms, subentire to ± strongly toothed in the upper 1/2-1/3; costa ending 1-3 cells below the apex, green in young leaves, often black or rarely red in older leaves; upper cells linear-rhombic to linear-rectangular often vermicular, (35)-40-80-(105) um long, 6-9-(11) um wide, rectangular near the base (3-6: 1); marginal cells similar to the median; asexual propagula numerous to few in the upper leaf axils of sterile shoots, often clustered in a few scattered leaf axils and scarce in the others, fewer but often present on fertile shoots, narrowly to broadly obconic when young (fig. 40: 8), ± oblong-obovate when older (fig. 40: 12-14), typically 300-500 um long, but often only clusters of young propagula ((0)-150-300 um long) or single older propagula (400-650 um long) present, with 3-5-(8) lanceolate, laminal leaf primordia present at the apex or sometimes lower on large, bulbiform propagula, the primordia arising a laminal appendages and never as peglike outgrowths, green when young, brown or more often red-brown when older, opaque; perigonia bulbiform, terminal on unbranched or once innovating stems; perigonial bracts variable in length, abruptly acute to ± longly acuminate from an ovate, concave, ± red-brown base, usually strongly toothed near the apex; costa ending in the acumen or 1-3 cells below; perichaetia terminal on unbranched or occasionally once innovating stems; perichaetial bracts to ca. 3.0 mm. long, lanceolate to linear-lanceolate, often red at the base; costa strong, ending in the apex or shortly before; median cells on average, longer and narrower than those of the vegetative leaves, linear-rectangular to linear-rhombic, ca. 75-115 um long, 5-6 um wide, thin walled; margins revolute from above the base to just below the apex, toothed near the apex. Dioicous; sporophytes infrequent; seta 1.5-3.0 cm. long, red to orange-red; capsules positioned 95°-170° from the vertical, 1.5-3.0 cm. long, short - to ± elongate pyriform, with a well developed neck, the neck often ± shrunken when dry; exothecial cells longitudinally elongate and ± rectangular to irregularly isodiametric, 23-50 um long, 15-26 um wide, with strongly sinuose walls, especially when dry, less so when moist, gradually to ± abruptly smaller and less sinuose near the mouth; stomata numerous in the neck, phaneropore, (30)-

33-39-(42) um long; annuli well developed, of 2-(3) rows of cells, remaining attached to the urn or the operculum, sometimes separating irregularly or rarely ± revolvable; opercula convex to conic, apiculate to umbonate; exostome teeth 16, yellow to yellow-brown above, darker below, lanceolate, ± narrowly acute, coarsely papillose in the upper 1/3, more finely papillose below; endostome segments 16, hyaline, keeled and broadly perforate; cilia (0)-1-3 between the segments, long, ± nodulose, sometimes short; spores baculate to clavate, (14)-16-21-(24) um; chromosome number = 11 (Danyikiv and Vysotska 1975 - voucher not seen).

Nomenclature: During most of the nineteenth century, the majority of bryologists included this species within their specific concept of *P. annotina*, and, in fact, Hedwig's type specimen of *Bryum annotinum* includes a few shoots of *P. andalusica* in mixture with the plant known to later authors as *Bryum annotinum* Hedw. It has been claimed by some (e.g. Buch 1906, Koch 1951, Lewis & Smith 1978), that when Lindberg (1871) published the name *Lamprophyllum annotinum*, he applied the name exclusively to this species. However, an examination of all the specimens determined by Lindberg as *Lamprophyllum, Pohlia, Webera* or *Bryum annotinum* (H-SOL) proves that he had a composite concept of the epithet, *annotina*, applying the name to several species, including those presently known as *P. annotina*, *P. andalusica*, *P. bulbifera* and *P. filum* (see section on nomenclatural history of the group). Consequently, *Lamprophyllum annotinum* (Hedw.) Lindb. is considered homotypic with Hedwig's *Bryum annotinum*, for which it is considered a new combination in the genus *Lamprophyllum*.

Höhnel (1895) described *Webera andalusica* from the Sierra Nevada Mountains of southern Spain, but his species was ignored by bryologists after Brotherus (1903) made the combination *Pohlia andalusica* (Höhnel) Broth. in the first edition of Engler & Prantl's *Naturlichen Pflanzenfamilien*. Andrews (1935) did not mention the name in his revision of *Pohlia* in North America. In his protologue of *W. andalusica*, Höhnel compared the species to *W. commutata* Schimper and *W. carinata* (Brid., Boulay) (sic), saying that it is most similar to the latter species. Höhnel provided an extensive description for *W. andalusica*, and discussed the occurrence of thin, green, leafless "pseudopodien" in the leaf axils of sterile shoots. It is likely that he was referring to the propagula which are present in a specimen which he determined (FH-Schiffner !). Loeske annotated the same specimen in 1909, saying that he thought it was a very interesting carinate form of *P. cruda* or *P. longicolla*, but compared the propagula to those of *P. rothii* (Corr.) Broth. (sic). *Pohlia andalusica* (= *P. rothii* of Loeske) rather frequently forms five-ranked, carinate expressions when growing in alpine situations, and the type specimen has propagula which agree closely with other specimens of the species. Consequently, although the specimen is unusually carinate and five-ranked, it is clearly conspecific with the plant known to later authors as *P. rothii*, and is the earliest name I can document for this species.

During the preparation of his treatise on asexual reproduction in mosses, Correns (1899) realized that bryologists had been using the epithet, *annotina*, for two distinct species of *Pohlia* (Correns used *Webera* for the genus). He thought that in addition to *P. annotina sensu* Hedwig, the name was also being applied to an as yet undescribed species, and consequently proposed the name *Webera erecta* A. Roth *ex* Correns for this taxon. As was noted by Lewis and Smith (1978), Correns' plate (1899, plate 95) illustrating *W. erecta* is very characteristic of *P. filum*, a species described in 1876 by Schimper (as *Bryum*). Lewis and Smith (1978) mentioned that they had examined a specimen labelled *Webera erecta* by Correns, and it consists of *P. filum* and *P. proligera* in mixture (as they did not distinguish *P. annotina* and *P. proligera*, it is unclear to which presently recognized species they applied the latter name). According to Lewis (in litt.), the specimen is in the herbarium of K.G. Limpricht (BP), and there is no specimen labelled *W. erecta* by Correns in his own herbarium in Munich (Hertel in litt.). Although I have not examined the specimen labelled *W. erecta* by Correns, it is still possible, on the basis of Correns' illustration (1899, plate 95), to confidently conclude that his *W. erecta* is conspecific with *P. filum*.

Soon after publishing *W. erecta* A. Roth *ex* Correns, Correns realized that the name was predated by *W. erecta* (Limpr.) Lindb. (1892). Correns therefore proposed (*in* Limpricht & Limpricht f. 1902) a *nomen novum, W. rothii*, to replace *W. erecta* A. Roth *ex* Correns. According to article 7 (ICBN), as a *nomen novum, W. rothii* is homotypic with the name it replaces, *W. erecta* A. Roth. *ex* Correns, and since *W. erecta* is presently considered to be a taxonomic synonym of *Pohlia filum* (= *Bryum filum* Schimper, 1876), so is *W. rothii*. For this reason, *W. rothii* is considered to be synonymous with *P. filum*, although recent authors have applied the name to that species presently known as *P. andalusica*. The nomenclature of *P. rothii* and *P. erecta* is discussed in greater detail on pages

In 1901, Grebe published a new variety; *Webera annotina* Bruch (sic !) var. *glareola* Ruthe & Grebe, which he had collected in 1893 and again in 1897 and 1898 (Grebe 1901). The plants were gathered from a rather xeric habitat on some rock rubble (Steinschutthalden) around an old copper mine in "Westfalen bei Marsberg." According to Grebe, he was immediately struck by the dense, compact habit of the plants which, he ~~said~~, was unlike any other indigenous *Pohlia* species. After a thorough examination of the morphological attributes of his new form, however, Grebe concluded that the plants agreed in all anatomical features (including the production of axillary propagula) to *Webera annotina* and differed only in its habit and stature. He suggested, therefore, that his collections represented a new variety of *W. annotina*. Ruthe, to whom Grebe sent specimens for his opinion, responded that they seemed to represent a "gut Standorts-Abänderung" of *W. annotina* and agreed as to its varietal status. Neither author made any distinction in the form of the propagula between the var. *glareola* and typical *Webera annotina*. An examination of several syntypes (lectotype: Kassel-Grebe !) revealed that *W. annotina* var. *glareola* is a species distinct from *Pohlia annotina* (Hedw.) Lindb., and corresponds to the plant which some recent authors have referred to as *P. rothii* (e.g. Lewis & Smith 1978, Smith 1978) and which is presently known as *P. andalusica*. Judging from specimens in Grebe's herbarium (I have examined 27 specimens named *Webera annotina, glareola, rothii* or *hercynica* from his collection - KASSEL), it is evident that Grebe did not consistently distinguish *P. annotina sensu* Hedwig from the plant presently known as *P. andalusica*, except by its compact habit. That is, he, and probably most other bryologists of the day, still did not realize that two taxa, distinguishable by the morphology of their propagula, were sharing the name *Webera annotina*. Under the epithet *glareola*, he included very compact xerophytic forms of the species, while as *W. annotina* he classified very lax forms of the same taxon. For intermediate "Standorts-Abänderung" (habitat modifications) he applied the names *Webera rothii* or *W. hercynica* ! Apparently, the "true" *Pohlia annotina* (Hedw.) Lindb. was uncommon in the flora with which Grebe was most familiar. Several specimens labelled *W. annotina* in his herbarium that actually are *P. annotina sensu* Hedwig (mixed with more frequent collections of *P. andalusica* incorrectly named) indicate that he did not conceptually distinguish these from slender forms of *P. andalusica*. Also included as the var. *glareola* in Grebe's herbarium are several specimens representing compact, xeromorphic forms of other species. The first specimen collected by Grebe in 1893 seems to be sterile *Bryum caespiticium* Hedw., juding by the compact, caespitose habit, the weedy collection locality, and the leaves with excurrent costae, faintly developed, unistratose border, and elongate, more or less incrassate upper-median leaf cells (cf. Nyholm 1958). Two other specimens labelled *W. glareola* are xerophytic modifications of *Pohlia nutans* (Grebe labelled most of his specimens *W. glareola* even though the name was eventually published at the varietal level). On the other hand, 9 out of 12 specimens labelled *W. glareola* by Grebe are *P. andalusica*, and Ruthe and

Grebe's reference to axillary propagula in the protologue of *W. annotina* var. *glareola* makes it clear that they did not intend the epithet for either *Bryum caespiticium* or *Pohlia nutans*. For this reason, I have chosen to lectotypify the var. *glareola* with one of Grebe's 1898 syntypes. This specimen corresponds in every respect to *P. andalusica*.

Limpricht (1902) elevated Ruthe and Grebe's variety to specific status as *Webera glareola* (Ruthe & Grebe *in* Grebe) Limpr., saying that the species "mit *gracilis* nachverwandt", (p. 726). He described *Webera glareola* as having propagula single in the leaf axils, an observation which is incorrect since they invariably arise in clusters in the axils of leaves in this species (fig. 5: 5). Only on shoots in which most propagula have fallen from the stem are they found singly in the leaf axils (e.g. fig. 5: 5, lower leaf axils).

Brotherus (1903) made the combination *Pohlia glareola* (Ruthe & Grebe *in* Grebe) Broth., but the publication included an orthographic error such that the name was spelled as *P. glaveola*. When making his new combination, Brotherus referred to Ruthe and Grebe as authors of the basionym and cited the type locality (Marsberg), so there need be no confusion as to the plant for which the name was intended.

Warnstorf (*in* Bauer 1913) described *P. hercynica* based on Bauer's *Musci Europeai exsiccati* no. 907 (not no.

906 as cited in *Index Muscorum*). The name was published in spite of Loeske's opinion that the plant represented "ein luxurient Wasserform" of *P. rothii (= P. andalusica)*. I interpret the plant as a phenotypic modification of *P. andalusica*, and have consequently given it no formal nomenclatural recognition.

In view of the historical confusion surrounding the names *Webera erecta* and *Webera* (or *Pohlia*) *rothii*, it seems fortunate that the earlier name, *P. andalusica* (Höhnel) Broth. has come to light. Hopefully this completely separate name will lead to a more consistent understanding of this species.

Distribution: (Figure 38). In the mountains of Western North America, *P. andalusica* is known from scattered localities in the Rocky Mountains from Colorado (Gilpin Co.) in the south through Alberta to the Yukon Territory and the Brooks Range of Alaska in the north. It is also known from a few localities in the Cascade and Olympic Mountains of Washington, but has not yet been collected further south in the Sierra Nevada range of California. *Pohlia andalusica* is also known from Great Bear Lake, Northwest Territories. In eastern North America, *P. andalusica* is apparently common in the Adirondack Mountains of New York, and extends south to Long Island, New York and Monroe Co., Pennsylvania. It occurs occasionally in the maritime provinces of Canada, and is seemingly disjunct on Baffin Island in the eastern arctic. Non North American specimens have been examined from Austria, Czechoslovakia, Finland, Germany, Greenland, Netherlands, Norway, Poland, Spain and Sweden, and Lewis and Smith (1978) reported this species from Denmark.

Selected Specimens Examined: Exsiccati. Bauer, Musci Eur. Exs. 321 as *P. rothii* (F, BH, COLO), 907 a as *P. hercynica* (WTU, COLO, H), 907 b as *P. hercynica* (H, ALTA), 912 as *P. rothii* (WTU, F. COLO), 1099 b as *P. rothii* (WTU, F, COLO); Breutel, Flora Germ. Exs. 286 as *B. annotinum* (BP); Brotherus, Bryotheca Fennica 74 as *P. annotina* (F); 4098 as *W. annotina* (COLO); Mougeot, Nestler, & Schimper, Stirpes Cryptog. Vogeso-Rhenanae 928 as *B. annotinum* (COLO); Pilous, Musci Czechosl. Exs. 708 as *P. annotina* (F, US), 1082 as *P. annotina* (F, US), 82 as *P. annotina* (CAS); Rabenhorst, Bryoth. Eur. 968 as *B. annotinum* (BP). Canada. *Alberta:* Jasper Nat. P., Maligne Lake area, banks of Bald Mountain Trail, *Shaw 2840* (ALTA). *British Columbia:* Revelstoke area, summit of Mt. Revelstoke, subalpine meadows, *Shaw 2811* (ALTA). Glacier National Park, top of Avalanche Crest Trail, *Shaw 2157* (ALTA). *Labrador:* Head of Kangalaksiorvik Fiord, 59°21-23'N, 64°00'W, *Weber 1519C* (NFLD). Twin Falls area, Scott Falls, 53°30'N, 64°32'W, *Brassard 6397* (NFLD). *New Brunswick:* Glouster Co., 5 mi.

(= 1 mi. = 1.6 km.) W. of Sheila, *Ireland 14288* (CANM). Victoria Co., 10 mi. S of Nictau, *Ireland 12852* (CANM). Kings Co., 3 mi. SE of Summerville, *Ireland 13911* (CANM). *Newfoundland:* Along Robinson River, ca. 8 mi E of Transcanada Hwy., 48°12'N, 58°37'W, *Weber 2285* (NFLD). Cataracts Prov. P., 7 km. WNW of Colinet, *Brassard 1129* (NFLD). *Northwest Territories:* Great Bear Lake, NE tip of Hornby Bay, *Steere 10498C* (NY). Baffin Island, Perry Bay, Meta Incognita Peninsula, 61°58'N, 66°30'W, *Fife 1120* (NFLD). *Nova Scotia:* Shelbourne Co., 3 mi. N of Upper Clyde R., 43°54'N, 65°28'W, *Ireland 12373* (CANM). *Prince Edward Island:* Prince Co., 5 mi. E of Richmond, *Ireland 10318* (CANM). Queens Co., 2 mi. S of Melville, 45°59'N, 62°50'W, *Ireland 13838* (CANM). Kings Co., 3 mi. NE of Summerville, 46°14'N, 62°44'W, *Ireland 13911* (CANM). *Quebec:* Terrebonne Co., S of Lac Mercier, *Crum 9956* (MICH). U.S.A. *Alaska:* Endicott Mtns., SE end of Chandler Lake, *Steere 18199* (NY). *Colorado:* 5 mi. W of Ward, *Hermann 27503* (DUKE). Gilpin Co., SE slope of James Peak, *Weber* 1969 (COLO). *Massachusetts:* Mt. Greylock area, *Andrews,* 1903 (BH). Merrimac, *Huntington,* 1901 (MIN). *Montana:* Lincoln Co., Leigh Cr. at Snowshoe Mine, *Gill 95* (CANM). *New Hampshire:* Willey House, Crawford Notch, *Smith & Miller 35683* (NYS). *New York:* Essex Co., Wilmington Notch, *Smith & Miller 33630* (FH). Franklin Co., 1.4 mi WSW of Franklin Falls, *Smith & Miller 35590* (NYS).

Pennsylvania: Monroe Co., *Johnson*, 1952 (WTU). *Utah:* Duchesne-Summit Co. border, near Mirror Lake, *Flowers 2086* (CANM). Duchesne Co., Ottoson Basin, *Flowers 9654* (COLO). *Washington:* Clallam Co., Olympic Nat. P., Obstruction Peak area, *Shaw 2156* (ALTA). Pierce Co., Mt. Rainier area, Paradise Point, *Shaw 2398* (ALTA). *Wyoming:* Teton Co., Grand Teton Nat. P., 7 km. W of Teton Park Rd. on Signal Mtn. Summit Rd., *Shaw 2704* (ALTA). Yellowstone National Park, banks of Crawfish Lake Trail at Moose Falls, *Shaw 2710, 2713* (ALTA).

When well developed, *P. andalusica* is characterized by its 1) clustered, obconic to oblong-obovate, green to red-brown, mostly opaque propagula having conspicuous, ovate-lanceolate to lanceolate, laminal leaf primordia and 2) leaves with a distinct sheen when dry. This species has been variously confused with *P. drummondii, P. filum* and *P. annotina* in the past, and Correns (1899) considered *P. andalusica* to fall within his concept of *P. drummondii* (see pages 99-100). Nyholm (1958) likewise interpreted it (as *P. rothii*) as a small, lowland form of *P. drummondii*. While propagula of these two species can be extremely similar at times, *P. andalusica* differs from *P. drummondii* in the following features: 1) propagula arising in clusters, usually obconic and gradually narrowed to the base, green when young, red-brown when older, but rarely cherry-red as in *P. drummondii;* 2) plants more slender, leaves more erect, less strongly carinate when dry and 3) stems paler in pigmentation, lacking the red coloration characteristic of *P. drummondii*. Although propagula of *P. andalusica* and *P. drummondii* can be very similar at certain stages of their ontogeny, they reach those stages via different developmental pathways. Shoots of *P. drummondii* typically produce single propagula in 2-5 leaf axils scattered along the stem. Young propagula dissected from the uppermost leaf axils are pale, hardly longer than wide and already have well developed, laminal leaf primordia (e.g. fig. 34: 1). They look just like very young branch buds, except that they are abruptly narrowed to the base where they are attached to the stem and are deciduous. Shoots of *P. andalusica* typically produce clusters of propagula in 2-4-(5) upper leaf axils, with few or no propagula produced in the remaining axils. Because the individual propagula are much broadened from the base, and because all the propagula in a cluster arise from a small "launching pad" in the leaf axil, the clusters often seem to radiate outward like a propaguliferous explosion stopped in mid-motion (e.g. see fig. 5: 5). Each young propagulum of *P. andalusica* is strongly obconic, considerably longer than wide, and has well developed leaf primordia which arise as laminal appendages (fig. 40). In early stages of development during which the propagula of *P. andalusica* are clearly obconic and clustered, there need be no confusion between this species and *P. drummondii*. However, as shoots of *P. andalusica* become older (e.g. later in the same season), many of the propagula gradually fall free. Sometimes only a single propagulum is left on the stem, and it may be large (ca. 500 um long) and oblong (e.g. fig. 40: 12-14) rather than obconic. Such shoots may be difficult to distinguish from *P. drummondii,* but in no sense should they be considered intermediate forms between the two species. My own culture studies, and those of Lewis (1976), show that plants with clustered propagula reproduce similar plants with clustered propagula, as do plants with single propagula reproduce their own kind in culture. This kind of ontogenetic convergence in the form of the propagula of *P. andalusica* and *P. drummondii* is quite distinct from actual intergradation between the two species, although it can sometimes make specimens a serious problem to determine. For that I apologize! Shoots of *P. andalusica* with only a single propagulum can be distinguished by the red-brown color and smaller size (mostly $<$ 500 um) of the propagulum, the leaf primordia which are generally more restricted to the apical region (e.g. fig. 40), the more nearly erect, less strongly carinate leaves and the slender size and paler pigmentation of the plants. Alpine forms of *P. andalusica* (including the type specimen) sometimes have leaves arranged evenly five-ranked down the stem. I have never examined such expressions in *P. drummondii*. Most important in many cases is that herbarium packets with *P. andalusica* bearing single propagula often have many of the smaller, obconic propagula which have fallen into the debris within the packet.

Of the species in which propagula arise in clusters, *P. andalusica* is unique in having the clusters in only a few scattered leaf axils rather than being evenly distributed along the upper half of the stem. This species is clearly very closely related to *P. drummondii* which also has propagula found in just a few upper leaf axils. As noted above; however, *P. drummondii* has the propagula arising singly in the leaf axils. Ontogenetically, *P. andalusica* is the "missing link" between those species with single propagula, and those with clustered propagula in that they occur in only a few leaf axils (cf. *P. drummondii* and *P. filum*), but they arise in clusters.

Of the species with clustered propagula, only *P. andalusica* and *P. bulbifera* have leaf primordia which arise as laminal appendages rather than as peglike outgrowths. *Pohlia bulbifera* is distinguished from *P. andalusica* by its typically wide-spreading, glossy leaves, and by its clusters of sphaeroidal to slightly oblong or rarely obconic propagula. The arrangement of the primordia of *P. bulbifera* propagula are unique, being concave and forming a dome over the apex, this feature giving the propagula their sphaeroidal shape (see under that species). Wilczek &

Demaret (1970) and Lewis & Smith (1978) noted that when freshly wetted, propagula of *P. bulbifera* often trap an air bubble among the domed primordia and suggested that this is a useful criterion on which to distinguish that species from all others. Unfortunately, young propagula of *P. andalusica* sometimes also have trapped air bubbles, so that I find this feature to be unreliable for consistently distinguishing *P. bulbifera* from *P. andalusica*. In practice, the two are usually readily distinguished by the shape of their propagula and on the habit of the plants. Although the leaf primordia of *P. annotina* propagula arise as peglike outgrowths, occasionally on much older, bulbiform propagula they may become more or less laminal by a limited number of cell divisions of the peglike primordium (e.g. see fig. 54: 23-26 and the discussion under *P. annotina*). Such propagula can be superficially similar to those of *P. andalusica* but differ in their strongly translucent appearance, and the primordia are often the same (or similar) color as the propagulum body, consequently appearing less strongly differentiated (visually) from the body. Plants of *P. annotina* are quite dull when dry and strongly contrast with the glossy appearance of *P. andalusica*.

4. *P. tundrae* J. Shaw *Spec. Nov.* (to be validated in the future). Holotype: Colorado, Larimer Co., Rocky Mountain National Park, ca. 5 miles west of Milner Pass on Hwy. 34,

40-25'N; 105-42'W, Shaw 2681 (ALTA). (Isotype: Herb. J. Shaw).

Plants scattered singly or more often forming dense, compact mats on alpine soil, occasionally more lax and elongate in protected areas, with a distinct gloss when dry; stems 2-5-(15) mm. high, green above, red or often ± black below, simple or sometimes once innovating at the base when sterile, often innovating once or twice below the perigonia or perichaetia when fertile; leaves erect to ± spreading when dry, spreading to ± erect when moist, (0.6)-0.8-1.1-(1.4) mm. long, (0.2)-0.3-0.4-(0.5) mm. wide, narrowly- to broadly lanceolate, acute, ± decurrent by 2-5 linear-rectangular cells or often nondecurrent on compact forms; margins plane to ± reflexed when dry, plane when moist, subentire to ± strongly toothed in the upper 1/2-1/3; costa ending 2-4 cells below the apex, rarely in the apex, green on young leaves, often becoming ± black on older leaves, very rarely red; upper cells rectangular or rhombic to linear-rhombic, sometimes ± vermicular, thin-walled, (45)-55-75-(100) um long, (6)-7-9-(11) um wide, ± rectangular to rhombic at the base, 3-6: 1, sometimes ± quadrate at the insertion; marginal cells similar in shape to the median, occasionally slightly narrower; asexual propagula numerous in the uppermost leaf axils of sterile shoots, rarely scarce on compact, alpine forms, absent from fertile plants, arising in clusters in each leaf axil, narrowly to broadly cylindric, rarely narrowly obconic, abruptly to gradually narrowed to a multiseriate stalk (usually remaining attached to the stem), 275-500-(900) um long, 60-90-(150) um in diameter, 3-5 cells thick or becoming broader and ± bulbiform when old, hyaline, green, or ± red when young, red to ± opaque red-brown when old and bulbiform, with 3-5-(7) lanceolate to ovate-lanceolate, laminal leaf primordia near the apex or often lower on the propagulum body, appearing conspicuous and often flexuose, arising as elongate, peglike outgrowths, but rapidly differentiating to form laminal appendages; perigonia bulbiform, conspicuous, terminal on short, simple stems, or the stems innovating once below the perigonia; perigonial bracts broadly ovate, abruptly acute to ± longly and narrowly acuminate from an ovate, concave, ± red-brown base, toothed above the shoulders; costa ending 1-3 cells below the apex, in the apex, or occasionally excurrent as a short mucro; perichaetia terminal on simple stems, rarely the stems innovating once- (twice) below the perichaetia; perichaetial bracts narrowly to broadly lanceolate, to 2.0-(2.5) mm. long, often red at the base; costa ending in the apex or 1-3 cells below; margins ± recurved from above the base to just below the apex, toothed in the upper 1/3; median cells longer and narrower than those of the vegetative leaves, to 110 um long, 5-7-(9) um wide, thin walled. Dioicous; sporophytes rare; seta 1.0-1.5 cm. long, orange to orange-red; capsule positioned 95°-140° from the vertical, short to ± elongate-pyriform, with a ± well developed neck, often ± shrunken when dry; exothecial cells longitudinally elongate and ± rectangular to irregularly isodiametric, 25-50 um. long, 15-30 um. wide, with strongly sinuose walls, especially when dry, less so when moist, gradually smaller, thicker walled and less sinuose near the mouth, more regularly isodiametric in the neck, ± abruptly long-rectangular just above the seta; stomata numerous in the neck, phaneropore, (27)-30-40-(48) um. long; annuli well developed, of 2-(3) rows of cells, remaining attached to the urn or the opercula, sometimes separating irregularly, rarely readily revolvable; operculum conic and often apiculate, rarely umbonate; exostome teeth 16, yellow to yellow-brown above, often darker below, lanceolate, ± narrowly acute, coarsely papillose in the upper 1/3, more finely papillose below; endostome segments 16, hyaline, keeled and broadly perforate; cilia (0)-1-3 between the segments, rudimentary, short, or sometimes elongate and ± nodulose; spores baculate, (17)-21-24-(30) um.

Distribution: (fig. 41). At present, *P. tundrae* is known only from western North America, although the species may yet be found in Asia with further study of appropriate specimens. An incomplete survey of the European herbarium material of the propaguliferous Pohlias has not yielded any records for this species. In North America, *P. tundrae* is a frequent species of alpine tundra in the western cordillera south of the maximum extent of glaciation, and seems to have been undercollected in the past. In the central Rockies, it has been collected from southern Colorado (San Juan Co.) and southern Utah (Garfield Co.) northward to Wyoming (Teton and Big Horn Co.) and Idaho (Custer Co.). In the Sierra Nevada Mountains it has been collected from California (Tulare and Inyo Co.) in the south, and probably occurs along the full length of that range. It is also known from Oregon (Mt. Hood) and Washington (Mt. Rainier). In addition, there are several disjunct localities presently known for this species, two in northernmost British Columbia, and two in southern Alaska.

Selected Specimens Examined: CANADA. *British Columbia:* Mile 84, Haines Highway, alpine meadow, *Crum* and *Schofield 9157* (CANM). Atlin area, ca. 16 km. NE of Surprise Lake on rd. to Mt. Barhan, *Shaw 3293* (ALTA). U.S.A. *Alaska:* Kenai Peninsula, 1 mi. (1 mi. = 1.6 km.) S of Ninilchik, Deep Creek Wayside, *Vitt 18441* (ALTA). Cantwell area, 32 km. N of Cantwell on Hwy. 3, *Shaw 3883* (ALTA). *California:* High Sierras, *Koch 1386* (BH). Frenso Co., jct. Nilgard Branch with Bear Cr., *Raven*, 1954 (CANM). Tulare Co., Primrose Lake, *Howell,* 1949 (CAS). Bakeoven Meadows, *Howell* 1950 (CAS). Inyo Co., W of Army Pass, *Koch H 138a* (MICH). *Colorado:* Pitkin Co., 17 mi. SE of Aspen, 10,800 ft., *Hermann 24458a* (COLO). Aspen area, *Shaw 2553* (ALTA). Chaffee Co., 16 mi. W of Nathrop, above St. Elmo, 10,000 ft., *Hermann 24491* (COLO). Clear Creek Co., 6 mi. SW of Silver Plume, Steven's Gulch, 12,000 ft., *Hermann 24491* (COLO). Loch Lomond, *Weber, Koponen & Nelson* 1972 (COLO). Larimer Co., 9 1/2 mi. SW of Rustic, 9600 ft., *Hermann 26656* (COLO). Rocky Mountain Nat. P., 5 mi. W of Milner Pass on Hwy. 34, *Shaw 2681* (ALTA). Grand Co., 8 mi. NE of Winter Park, *Hermann 25056* (COLO). Boulder Co., Niwot Ridge, 11,000 ft., *Weber & Nelson* 1972 (COLO). 2 1/2 mi. WNW of Allenspark, *Hermann 25502*. San Juan Co., 6 mi. N of Silverton, *Hermann 24416* (COLO). Gilpin Co., 20 km. W of Rollinsville on Corona Pass Rd., *Shaw 2605* (ALTA). 5 km. E of Corona Pass, *Shaw 2629* (ALTA). Near trail head to Arapahoe Pass, *Shaw 2652* (ALTA). *Idaho:* Boise Nat. For., near Sulfur Springs, *MacFadden 19228* (BH). Salmon Nat. For., Gibbonsville area, *Shaw 2718* (ALTA). *Montana:* Belt. Mountains, R.S. Williams (WIS). *Nevada:* Washoe Co., Mt. Rose, *Lawton 3071* (WTU). *Oregon:* Clackamas Co., Mt. Hood area, Salhalie Falls, *Shaw 2532* (ALTA). Union Co., 20 mi. SE of Union, 5000 ft., *Hermann 18873* (CANM). *Utah:* Duchesne Co., Uintah Mtns., near Mirror Lake, *Flowers 7393* (COLO). Uintah Mtns., Ottoson Basin, *Flowers 9667* (COLO). Garfield Co., Aquarius Plateau, 11,000 ft., *Flowers 7314* (COLO). Summit Co., Uintah Mtns., Bald Mtn., *Flowers 2101* (COLO). Henry's Fork, *Flowers 1329* (COLO). Juab Co., Deep Creek Mtns., Thomas Cr., *Lindsay 5858* (COLO). *Washington:* Pierce Co., Mt. Rainier area, Paradise Point, *Shaw 2421* (ALTA). *Wyoming:* Yellowstone Nat. P., Norris Geyser Basin, *T.C. Frye,* 1925 (WTU). Teton Co., 7 km. W of Teton Park Rd. on Signal Mtn. Summit Rd., *Shaw 2709* (ALTA). Banks of Bradley Lake, *Shaw 2701* (ALTA). 23 mi. E of Moran, *Hermann 25542* (US). Johnson Co., Bighorn Nat. For., *Weber, Kunkel* & *Munger* 1974 (COLO).

Pohlia tundrae is characterized by 1) its compact growth form with short stems, 2) leaves with a distinct sheen when dry, and 3) its large (> ca. 300 um long), cylindric to gradually and narrowly obconic propagula with conspicuous, laminal leaf primordia. *Pohlia tundrae* is a characteristic moss of mesic alpine tundra in western United States, and usually forms short, compact turfs with stems no more than 2-4 millimeters high. When growing in shaded subalpine habitats, the stems may be more lax and elongate, but such occurrences are quite infrequent. The leaves consistently have a strong sheen when dry, although when the plants are very short and compact, this feature is not so apparent as when the stems are elongate. I have not encountered plants with distinctly five-ranked, carinate leaves, as sometimes occurs in alpine populations of *P. andalusica* and *P. filum*. The leaves of alpine

P. tundrae populations tend to have the costa not forming a strong keel, and are typically erect to erect-spreading in a tufted rosette.

The propagula of *P. tundrae* are strikingly long and cylindrical, and extend well beyond the erect leaves of tufted plants. Occurring in dense axillary clusters, they give the plants a bushy appearance in the field under a hand lens, and are rarely few or absent. When well developed, the propagula average greater than 300 um long, and are straight, not at all vermicular, often up to 85-(100) um in diameter. Plants growing in shaded situations tend to have narrower propagula, and these may be somewhat flexuose when dry between the spreading leaves of such lax forms. In color the propagula are rather uniform, often whitish or hyaline on lax plants, but more typically red-brown on compact, alpine plants. When young, they are green, but rapidly take on a more reddish hue at an early stage of development. The leaf primordia arise as elongate, peglike outgrowths, but very soon after their initiation they become 2-4 cells wide at the base (fig. 43: 1) and shortly thereafter, truly laminal in form (fig. 11: 3, 43: 3, 4). On propagula large enough to be visible among the upper leaves, the leaf primordia are conspicuously lanceolate-laminal, quite flexuose (fig. 43: 5, 6), and may occur well down on the propagulum body as well as at the apex (fig. 43: 10).

Pohlia tundrae often grows intermixed with *P. drummondii* in alpine tundra habitats, and the two species can be difficult to distinguish in such situations in the absence of propagula. Fortunately, although propagula may be scarce on *P. drummondii* stems growing above treeline, they are usually present and conspicuous on *P. tundrae*. It is not uncommon to find a turf of compact Pohlias, some stems having clustered propagula, but completely intermixed with similar looking plants apparently lacking propagula. In most cases, the propaguliferous plants are *P. tundrae*, and the plants with only scarce propagula are *P. drummondii*. In such alpine situations, *P. drummondii* is often found with sporophytes, while sexual reproduction in *P. tundrae* is less frequent. Occasionally, *P. drummondii* plants are encountered with unusually narrow propagula, and these can be similar to forms of *P. tundrae* with atypically large, bulbiform propagula (e.g. fig. 43: 10). In *P. tundrae*, the propagula occur in clusters in the leaf axils, and usually have less of a red pigmentation than propagula of *P. drummondii*. On those rare occasions when specimens of *P. tundrae* completely lack propagula, the plants may be indistinguishable from *P. drummondii*. However, the two species usually differ subtly in pigmentation. The stems and sometimes the lower leaves of *P. tundrae* are often black when old, as opposed to the characteristic red pigmentation of *P. drummondii*. Unfortunately however, alpine populations of *P. drummondii* may be paler in pigmentation (e.g. pink stems) than lowland populations of the same species.

When growing below treeline in more shaded situations, *P. tundrae* may approach *P. proligera* in morphology. Such plants are often very glossy, and have clusters of long, narrow propagula which superficially resemble those of *P. proligera*. When moist, the propagula of such lax *P. tundrae* plants are longer, not vermicular, and diverge almost at right angles from the stem such that they extend well beyond the leaves. The propagula of *P. proligera* are considerably shorter, strongly vermicular, and form a dense, tomentum-like mass hidden by the more erect to erect-spreading leaves. Furthermore, the propagula of *P. proligera* have only one or two peglike, apical leaf primordia, while those of *P. tundrae* have conspicuous, lanceolate-laminal primordia often not restricted to the propagulum apex. Very narrow propagula of lax *P. tundrae* plants may have less well developed leaf primordia, but they are still at least 3-4 cells broad at the base (fig. 43: 3). When the two species grow intermixed (which is infrequent), they can seem to present a continuum in the morphology of their propagula, but it is possible to separate them, plant by plant, and assign them to one or the other species.

Pohlia tundrae has generally been named *P. annotina* var. *decipiens* in North American herbaria. Flowers (1973) illustrated *P. tundrae* in his moss flora of Utah and the west, and his specimens (COLO) are almost all *P. tundrae*. *Pohlia annotina* has not been collected in the Rocky Mountains south of Canada, and all reports of *P. annotina* var. *decipiens* from the mountains of Utah and Colorado are referrable to *P. tundrae* (reports of *P. annotina* var. *annotina* are mostly *P. camptotrachela*). *Pohlia annotina* may be distinguished from *P. tundrae* by its dull leaves, and slender habit. Its propagula, when narrowly elongate, approach those of *P. tundrae* in size and shape, but have peglike leaf primordia which are always restricted to the apical region. See figure 44 for a quantitative comparison of these two species. The habitats of these two species are entirely different (see pages 136-137), and they are quite unlikely to be found co-existing in the same habitat. Their geographic ranges scarcely overlap, and this can be useful in determining specimens thought to be one of the two.

5. *Pohlia bulbifera* (Warnst.) Warnst. Krypt. Fl. Brandenburg. 2: 429. 1904.

Webera annotina var. *angustifolia* Schimper, Syn. ed. 2: 401. 1876. Type:"Uleaborg, leg. W. Nylander" (type not seen).

Webera annotina var. *tenuifolia* Schimper, Syn. ed. 2: 401. 1876. Type: "Italia superiore usque in Lapponian" (type not seen).

Pohlia annotina var. *tenuifolia* (Schimper) Braithw., Brit. Moss F. 2: 152. 1892.

Webera bulbifera Warnst., Bot. Centralbl. 66: 230. 1896. Type: "Westpreussen ... bei Marienfelde ... von Grutter entdeckt." Neotype: "Sample no. 164, bank of River Fillan, Crianiarich, W. Perth. October 1967, leg. K. Lewis" (NMW !).

Bryum pseudo-carneum Kindb., Ottawa Naturalist 14: 88. 1900. Type: "Sable Island, Canada. Leg. Macoun" (Lectotype: S-Kindb. !; Isotypes: US, BH !).

Webera tenuifolia (Schimper) Bryhn, Nyt. Mag. Naturvid. 40: 34. 1902. *hom. illeg.*

Webera serrifolia Bryhn, Rev. Bryol. 29: 127. 1902. (based on: *Webera tenuifolia* (Schimper) Bryhn).

Webera pseudo-carnea (Kindb.) Macoun, Cat. Canad. Pl. 7: 246. 1902.

Pohlia serrifolia (Bryhn) Broth. *in* Engler & Prantl, Nat. Pfl. 1 (3): 552. 1903.

Pohlia pseudo-carnea (Kindb.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 551. 1903.

Pohlia tenuifolia (Schimper) Moell., Bot. Notis. 1907: 143. 1907.

Pohlia annotina var. *angustifolia* (Schimper) Podp., Cas. Moravsk. Mus. Zemsk,. Brno 13: 236. 1913.

Webera annotina var. *bulbifera* (Warnst.) Dix., Stud. Handb. Brit. Mosses ed. 3: 335. 1924.

Plants of medium-size, forming small to extensive turfs, often intermixed with other mosses, with a strong sheen when dry; stems 5-15-(25) mm. high, green to orange above, orange to ± red or almost black near the base, simple or sometimes once innovating near the base when sterile, simple or often innovating once below the perigonia when fertile; leaves wide-spreading to erect-spreading and flexuose when dry, wide-spreading when moist, (0.6)-0.9-1.3-(1.6) mm. long, 0.3-0.4-(0.7) mm. wide, narrowly- to broadly lanceolate or ovate-lanceolate, acute, mostly long decurrent by 2-4 linear-rectangular cells, less decurrent when the plants are more compact; margins plane, strongly toothed in the upper 1/3, often ± toothed to midleaf and sometimes to the base; costa ending 1-4 cells below the apex, green in young leaves, often red-brown to black in older leaves; upper cells rectangular or rhombic to rhombic to linear-rectangular or linear-rhombic, rarely vermicular, (45)-60-90-(105) um long, (6)-8-11-(13) um wide, variable in size and shape on a single leaf, rectangular near the base, 3-6:1; marginal cells similar to the medium except projecting as teeth; asexual propagula usually abundant in the upper leaf axils of sterile shoots, arising in clusters in each leaf axil, rarely appearing single on old shoots, absent from fertile plants, rather uniform in shape, sphaeroidal to obovate, abruptly narrowed to a multi-seriate stalk, mostly (150)-300-400-(520) um. in the longest dimension, green to yellow or sometimes yellow-orange or orange-red, opaque or ± translucent, often glossy when dry, with 4-5 broadly triangular, concave, laminal leaf primordia which form a rounded dome over the propagulum apex, the primordia arising as laminal appendages, never as peglike outgrowths, with bulging cell walls (fig. 11: 6); perigonia bulbiform, terminal on unbranched stems or the stems once innovating from just below the perigonia; perigonial bracts abruptly acute to ± gradually acuminate from an ovate, concave, ± red-brown base; margins ± strongly toothed near the apex; costa ending just below the apex or in the apex; perichaetia terminal on unbranched or rarely basally innovating stems, rather inconspicuous; perichaetial bracts to ca. 2.8 mm. long, lanceolate to linear-lanceolate, mostly ± red at the base; costa strong, filling the acumen or ± excurrent as a stout mucro; median cells on average, somewhat longer than those of the vegetative leaves, mostly thin-walled, to 115 um. long, sometimes vermicular; margins recurved from above the base to just below the apex, usually strongly toothed near the apex. Dioicous; sporophytes infrequent; seta 1.5-2.5 cm. long, orange to orange-red; capsules positioned 100°-180° from the vertical, 1.5-2.5 mm. long, ovate-pyriform, with a well developed neck which is ± shrunken when dry, tan or yellow to orange when mature; exothecial cells longitudinally elongate and ± rectangular to irregularly isodiametric, mostly 30-65 um. long, 20-36 um. wide, with strongly sinuose walls, especially when dry, less so when moist, gradually to ± abruptly smaller, less sinuose and sometimes transversely elongate and rhombic near the mouth, more nearly isodiametric in the neck, gradually to ± abruptly longer, narrower, and nonsinuose just above the seta; stomata numerous in the neck, phaneropore, (35)-45-55-(70) um long; annuli well developed, of 2-(3) rows of cells, remaining attached to the urn or the opercula, sometimes separating irregularly or rarely ± revolvable; opercula concave to conic and apiculate to rostellate; exostome teeth 16, yellow above, yellow to yellow-brown below, lanceolate, ± narrowly acute, coarsely papillose or rarely faintly striolate on the dorsal surface in the upper 1/3, more finely papillose below; endostome segments 16, hyaline, keeled and broadly perforate; cilia (0)-1-3 between the segments, long, ± nodulose, sometimes short; spores baculate to clavate, (17)-22-20-(35) um.

Nomenclature: As noted by Lewis and Smith (1978), when Warnstorf (1896) described *Webera bulbifera*, he cited *Webera annotina* var. *tenuifolia* Schimper (1876) and *W. annotina* var. *angustifolia* Schimper (1876) as synonyms.

I have included these varieties in the synonymy of *P. bulbifera* because of Warnstorf's (1896) comment, although type specimens for neither taxon could be located in the British Museum (Harrington in litt.).

Warnstorf (1896) described *Webera bulbifera* in connection with his review of Grütter's (1895) *Beiträge zur Moosflora des Kreises Schwetz*, and made the combination *Pohlia bulbifera* (Warnst.) Warnst. in 1904. No specimen labelled *Webera* (or *Pohlia*) *bulbifera* by the hand of Warnstorf could be located in Berlin (Nowack in litt.) although a specimen of *P. hercynica* Warnst. *in* Bauer (1913) *(= P. andalusica)* does exist in B- Warnstorf (Schultze-Motel in litt.). Correns (1899) reported having examined a duplicate from the type locality (Weisse bei Marienfelde, VII 1895. leg. Grutter) but that specimen apparently could not be found in Munich. It is likely that Warnstorf distributed duplicates to other bryologists of his day, and possibly an isotype will eventually be found (*ex* herb. Grütter?). Although Lewis and Smith (1978) noted that they had "seen a specimen collected and presumably named by Warnstorf" (Bauer, *Musci eur. exs.* no. 310), they chose to designate a specimen collected by Lewis (Sample no. 164, bank of River Fillan, Crianlarge, W. Perth. October 1967, leg. K. Lewis) as the neotype. I agree with them that the neotype agrees well with Bauer's exsiccata specimen, and in the absence of an isotype, this is presently considered the type specimen of *P. bulbifera*.

I can confirm Andrews' (1935) opinion that the type specimen of *Bryum pseudo-carneum* Kindb. (1900) falls within the morphological range of *P. bulbifera* (Lectotype: S-Kindb.!, Isotype:BH, US !).

Distribution: *Pohlia bulbifera* has been collected very sporadically in the mountains of western North America, but is much more frequent in northeastern United States and the adjacent maritime provinces of Canada. In the west, collections have been seen from Colorado (Boulder Co.), Alberta (Lesser Slave Lake area), a few localities in southern Alaska, and several in the central and southern Yukon Territory. From my own collecting in the western cordillera I think that these sporadic collections are indicative of *P. bulbifera*'s rarity in the west, rather than it's having been undercollected like many other North American Pohlias. In the eastern portion of the continent, *P. bulbifera* is decidedly more common than in the west, extending from New York and Massachusetts northward in the maritime provinces to Labrador;and westward to Wisconsin and northern Michigan. It is not yet recorded from arctic North America, although collections from Greenland and Iceland indicate that it may still be found in the northern portions of North America. *Pohlia bulbifera* has not been collected quite so far south in eastern United States as

P. andalusica, and does not extend nearly so far south as *P. annotina*. Non North American specimens have been examined from Austria, England, Federal Republic of Germany, Finland, Greenland, Iceland, Netherlands, New Guinea, Norway and Sweden.

Selected Specimens Examined: Exsiccati. North America: Macoun, Can. Musci 445 a as *W. pseudo-carnea* (US); Relinquiae Farlowianae 573 as *W. annotina* (BH, MICH, MO, US, WIS); Sull. & Lesq., Musci Bor. Am. (Ed. 1) 180 (MICH - in part). *Europe:* Bauer, Musci Europ. Exs. 310 as *P. bulbifera* (F, COLO, BH - in part); 1091 as *P. bulbifera* (F, COLO); Brotherus, Bryoth. Fenn. 129 as *P. bulbifera* (F, US); Husnot, Musci Galliae 874 as *P. annotina* (F, BH); Mikutowicz, Bryoth. Baltica 19 as *W. bulbifera* (US); 19a as *W. bulbifera* (US). Canada. *Alberta:* Lesser Slave Lake area, *Vitt 7309* (ALTA). *Labrador:* Twin Falls area, Scott Falls, 53°32'N, 64°32'W, *Brassard 6397* (NFLD). Churchhill Falls area, 53°36'N, 59°48'W, *Brassard 5512* (NFLD). Near Three Rapids Camp, 54°52'N, 59°48'W, *Brassard 11381* (NFLD). Esker-Churchhill Falls Rd., mi. 75 (1 mi. - 1.6 km.), 53°41'N, 64°51'W, *Brassard 6129* (NFLD). *New Brunswick:* Charlotte Co., 2 mi. E. of St. Andrew, *Ireland 13319* (CANM). King's Co., 2 mi. S of Nauwigewauk, *Ireland 13453* (CANM). York Co., 3 mi. N of Lake George, *Ireland 13016* (CANM). *Newfoundland:* Head of Dolland Bight, Hare Bay, 47°41'N, 56°34'W, *Tuomikoski 1357* (H). Gander, Bonavista North, 48°57'N, 54°38'W, *Tuomikoski 26* (H). Cataracts Prov. P., 7 km. WNW of Colinet, *Brassard 1114* (NFLD). Mouth of Bartlett's River, Pistolet Bay, White Bay, *Toumikoski 3951* (H). Baie Verte Peninsula, 6 km. N of intersection Trans Canada Hwy. & Hwy. 410, *Brassard 10997* (NFLD). Daniel's Harbor, *Palmen 4318* (H). *Nova Scotia:* Halifax Co., 3 mi. N of Musquodoboit, *Ireland 13139* (CANM). Sable Island, *Macoun,* 1899 (BH). *Ontario:* 8 mi. S of Dorset, *Miller & Smith 1052* (FH). Between Montreal River and Speckled Trout Creek, *Sharp,* 1962 (MICH). *Quebec:* 11 mi. S of Plessisville, *Crum & Williams 10451* (MICH). Parc du Mt. Tremblant, *Hermann 16861* (CANM). Montagne Tremblant Nat. P., Lac Monroe, *Raymond & Kucyniak,* 1953 (BH). Magdalen Islands, East Island, *Reilly 562* (MICH). Iles-de-la-Madaleine, Ile de l'Est, *Sloover 8171* (NFLD). *Yukon Territory:* McQuesten area, South Klondike Syrenite Basin, *Cambell 750* (CANM). U.S.A. *Alaska:* Ketchikan area, 9 km. N of Ketchikan at Ward Lake campground, *Shaw 1629* (ALTA). Juneau Quadrangle, 28 mi. WNW of Juneau, *Hermann 22107* (CANM). King Salmon, *Schofield 2780* (ALTA). Kodiak Island, NE of Kodiak, *Sharp 413* (TENN). Cordova Quadrangle, at Yukutat, *Hermann 21746* (US). Kodiak Isl., *Trelease 2222* (MO). *Colorado:* Boulder Co., 4 mi. W of Ward, *Hermann 23475* (COLO). Larimer Co., Rocky Mtn. Nat. P., *Hermann 25749* (US). *Maine:* Base of Mt. Katahdin, *Andrews,* 1950

(BH). 14 mi. NW of Rangeley, *Miller 1580* (NYS). Baxter State Park, *Miller 1622* (NYS). Piocataquis Co., 13 1/2 mi. N of Milo, *Hermann 19161* (UBC). *Massachusetts:* Relinquiae Farlowianae 573, Magnolia (FH). *Michigan:* Luce Co., Whitefish Pt., *Griffin 1* (TENN). Chippewa Co., 3 mi. NW of Homestead, *Crum,* 1969 (MICH). 4.1 mi. S of Paradise, *Miller 4015* (MICH). *New Hampshire:* White Mtns., Mt. Washington, *Miller 1654* (NYS). Road from Randolf to Glen Home, *Andrews,* 1918 (BH). Willey House, Crawford Notch, *Smith & Miller 35687* (NYS). Grafton Co., Grafton, *Hutchinson 357* (DUKE). *New York:* Franklin Co., 6 1/2 mi. E of Tupper Lake, *Hermann 13896* (US). Between Paul Smiths & Clear Lake Jct., *Smith 37351* (NYS). Essex Co., upper slopes of Mt. Whiteface, *Smith, Rogerson & Dean 49708* (FH). Tom Peck Lake, *Smith 37472* (NYS). Hamilton Co., Upper Brown Tract Pond, *Smith & Miller 36005* (NYS). Buttermilk Falls, Raquette Lake, *Smith 37142* (NYS). Greene Co., South Lake, Kaaterskill Falls, *Smith 36837* (NYS). *Vermont:* Washington Co., Maple Corners, *Hoisington,* 1976 (MICH). *Wisconsin:* Portage Co., Linwood, *Freckmann 1350* (MICH).

Pohlia bulbifera is characterized by its 1) leaves spreading to wide-spreading with a strong sheen when dry and 2) its clustered, sphaeroidal to obovate propagula with (3)-4-(5) broadly triangular, laminal leaf primordia which form a rounded dome over the propagulum apex. The outer cells of the propagula, unlike those of any of the species, are strongly bulging (fig. 11: 6), although this feature is not conspicuous under a light microscope. The shape of the propagula are quite uniform, consistently isodiametric to obovate. The sphaeroidal shape is the result of the unusual arrangement of the leaf primordia, which are almost whorled at the propagulum apex. The propagulum body is actually hemispheric, and the "upper" half of the sphaeroidal shape consists of the over-arched, concave leaf primordia (fig. 47). The propagulum apical cell is completely hidden by the leaf primordia. The primordia probably serve (or served in the past) to protect the growing point of the propagulum, but, as was pointed out by Correns (1899), the propagula of *P. bulbifera* do not grow by division of the apical cell after its earliest stages of growth. When germinating, *P. bulbifera* propagula produce rhizoids from which young gametophores arise, rather than elongating itself by its own apical cell (cf. *P. filum*, *P. andalusica* and *P. drummondii*). Quite possibly, the doomed primordia were more important in protecting the delicate apical region when this area was more important for growth and germination of the propagula (cf. Correns 1899).

Pohlia bulbifera has been interpreted consistently since Warnstorf described it in 1896. Before that time, most bryologists must have included *P. bulbifera* within their concept of *P. annotina*, since that was the only described species with clustered propagula (except for *P. proligera* which was described just a few years before *P. bulbifera*). For example, *P. bulbifera* is not uncommon in S.O. Lindberg's herbarium under the label *Lamprophyllum* or *Pohlia annotina*. On some packets he distinguished *P. bulbifera* as the var. *brevifolia* (but never published the name, to my knowledge).

Of the species with propagula arising in axillary clusters, only *P. tundrae, P. andalusica* and *P. bulbifera* have leaf primordia that are conspicuously laminal. All three species are normally quite glossy when dry, but *P. tundrae* is easily distinguished by its very long, linear-cylindric propagula. Propagula of *P. andalusica* and *P. bulbifera* are more similar to one another. Especially in dried herbarium specimens which have been slightly flattened through the years, propagula of *P. bulbifera* may appear to have more or less erect leaf primordia like those of *P. andalusica*. For the most part, by examining a number of propagula from a given specimen, however, it is usually easy to determine that those of *P. bulbifera* are normally concave and arched over the apex. The yellow to yellow-orange color of *P. bulbifera* propagula also contrasts with the typically red-brown color of *P. andalusica* propagula. In the rare event that propagula of *P. bulbifera* are scarce, the widely spreading leaves give the plants an entirely different aspect than plants of *P. andalusica* with their more or less erect leaves. See also under *P. andalusica* for a discussion of the differences between these two species.

6. *Pohlia andrewsii* J. Shaw *Spec.Nov.* (to be validated in the future). Holotype: Dawson area, 17 km. east of the Alaska-Yukon border on Hwy. 3. ca. 64-12'N; 138-56'W, Shaw 3619 (ALTA). (Isotypes: Herb. J. Shaw, Herb. A.C. Crundwell, S, BH).

Nomenclature: Because so many species of the genus *Bryum* have been described from high latitudes, it is difficult to say for sure that this species has not been described previously in bryological literature. However, I have examined type specimens for most *Pohlia* species published from arctic localities, and all *Pohlia* species from that region which are known to produce propagula. Consequently, I feel that it is appropriate to suggest the name *Pohlia andrewsii*. It is my pleasure to name this moss for Dr. A. LeRoy Andrews, who contributed greatly to our knowledge of the genus *Pohlia*, and whose herbarium I was able to study and learn from while beginning in bryology as an undergraduate at Cornell University.

Plants generally robust, forming small, isolated populations in soil-filled rock crevices, occasionally intermixed with other mosses, glossy when dry; stems 3-15-(35) mm. high, green above, green or ± red near the base, simple or sometimes innovating 1-(3) times from the base when sterile, simple or once innovating below the inflorescence when fertile; leaves erect to ± spreading and slightly flexuose when dry, sometimes ± carinate, when moist, ± spreading and sometimes carinate in elongate forms, more erect and plane when the plants are short and compact, (0.65)-0.85-1.30-(2.00) mm. long, (0.25)-0.30-0.40-(0.55) mm. wide, lanceolate to broadly lancolate, short- to gradually long acute, ± decurrent by 1-3 rectangular or rhombic cells, sometimes scarcely or not at all decurrent in compact forms; margins plane to somewhat reflexed when dry, plane when moist, ± strongly toothed in the upper 1/3-1/2, occasionally subentire, entire to subentire below; costa ending 3-5-(6) cells below the apex, green in young leaves, green or ± red to black in older leaves; upper cells rectangular or rhombic to linear-rhombic, occasionally vermicular, (35)-45-60-(85) um long, (6)-7-9-(11) um wide, thin-walled, rectangular at the base, 3-6:1, undifferentiated near the margin or sometimes somewhat longer; asexual propagula consistently present in the upper leaf axils of sterile shoots, usually present but few in number on perichaetial plants, arising in clusters in the leaf axils, oblong to linear-oblong on lax, elongate stems, oblong to isodiametric on short, compact stems, rarely more than three times as long as wide, typically 50-165 um long, but sometimes only a few older propagula present (> 170 um long), green when young, distinctly red when older, strongly translucent, with 1-3-(5), inconspicuous, often incurved, peglike or laminal leaf primordia near the apex, the leaf primordia generally inconspicuous, arising as short, peglike protuberances, usually becoming distinctly laminal with age, occasionally remaining peglike and rarely appearing rudimentary, never becoming elongate and finger-like (cf. *P. proligera* fig. 62); perigonia bulbiform, terminal on unbranched stems or the stems once innovating below the perigonia, perigonial bracts short to ± long acuminate from an ovate, concave, ± red-brown base, ± strongly toothed above the shoulders; margins sometimes ± recurved from above the shoulders to just below the apex; costa ending in the apex or 1-5-(6) cells below; perichaetia terminal on unbranched stems or sometimes the stems once (-twice) innovating below the inflorescence; perichaetial bracts to 2.5 mm. long, linear-lanceolate to lanceolate, often red at the base, costa strong, ending in the apex or 1-3 cells below; median cells, on average, somewhat longer than those of the vegetative leaves, 65-105 um. long, 6-8 um. wide, thin-walled; margins revolute from above the base to just below the apex, toothed in the upper 1/3, rarely subentire. Dioicous. Sporophytes infrequent, seta 1.5-3.0 cm. long, orange-red to red; capsules positioned 95°-140° from the vertical, 1.5-3.0 mm. long, short- to ± elongate-pyriform, with a well developed neck, sometimes almost as long as the urn, often shrunken when dry; exothecial cells longitudinally elongate and ± rectangular to irregularly isodiametric, 25-50 um long, 15-26 um wide, with strongly sinuose walls, especially when dry, less so when moist, gradually to ± abruptly smaller and less sinuose near the rim, gradually elongate-rectangular just above the seta; stomata numerous in the neck, phaneropore, (32)-34-48-(55) um. long; annuli well developed, of 2-(3) rows of cells, remaining attached to the urn or the operculum, sometimes separating irregularly or very rarely ± revolvable; opercula conic and usually apiculate; exostome teeth 16, yellow to yellow-brown above, darker below, lanceolate, ± narrowly acute, coarsely papillose in the upper 1/3, more finely papillose below; endostome segments 16, hyaline, keeled and broadly perforate, cilia usually well developed, (0)-1-3 between the segments, long, ± nodulose, sometimes short; spores coarsely baculate to clavate, (14)-16-19-(23) um.

Distribution: The presently known distribution of *P. andrewsii* includes arctic North America, northern Greenland, Spitzbergen and the south-central coast of Norway. It is likely that this species also occurs in arctic Asia, and that its distribution is truly circumpolar. In North America, *P. andrewsii* is known from the westernmost islands of the Aleution chain, and is widespread in arctic and subarctic Alaska, apparently extending no farther south than the Brooks Range on the mainland. In the Yukon Territory, it is frequent south to Keele Peak in the Hess Mountains wherever the bedrock is siliceous, a range that includes alpine tundra in sub-arctic mountains. In the Northwest Territories, *P. andrewsii* has been collected from the Mackenzie Mountains near the Yukon border, from Great Bear Lake, and from a few localities in the arctic archipelago. Its sporadic occurrence in arctic North America is probably because of, in part, very incomplete collecting in the area, and also because of its preference for siliceous soils which occur only in scattered localities. *Pohlia andrewsii* is known from two localities in Greenland (Cape York, Murraysö), and from several localities in Spitzbergen. Lindberg's (1867) report of *P. annotina* from Spitzbergen was based on specimens of *P. andrewsii* (H-SOL!). In Norway, this species is known from Omenberges, in Opdal (Bryhn 1885-H-SOL!).

Selected Specimens Examined: Canada: *Northwest Territories:* Great Bear Lake, E end of McTavish arm, *Steere 10298* (NY). Ellesmere Isl., near Doidge Bay, *Brassard 4190* (NFLD). 19 mi. (1 mi. = 1.6 km.) N of head of Baad Fiord, *Blake 8-1967* (CANM). Coburg Isl., E coast, *Blake 26 b* (CANM). Devon Isl., Sparbo-Hardy Lowland, *Vitt 6580* (ALTA). Mackenzie Mtns., Liard Range, *Horton 10735* (ALTA). Logan Mtns., Lake close to Nahanni R., *Horton 14372* (ALTA). Yukon Territory: Tombstone Mt. area, 6.5 mi. northeast of Tombstone Mtn., *Vitt 8105* (ALTA). Ogilvie Mtns., mi. 42, Dempster Hwy., *Vitt 6253* (ALTA). Hess Mtns., Keele Peak, *Vitt 15939* (ALTA). Keno Hill, *Vitt 16214* (ALTA). North Rackla Range, Gillespie Lake, *Vitt 16663* (ALTA). Southern Richardson Mtns., 'Lenense Lake, *Vitt 16252* (ALTA). Dawson area, 17 km. E of the Alaska-Yukon border on Hwy. #3, *Shaw 3619* (ALTA). Greenland: Cape York, N. slope, *Nutt,* 1940 (MICH). Murray-so, *Dusen 4383* (H). Norway, Opdal, Olmenberges, *Bryhn,* 1885 (H-SOL). *Spitzbergen:* Smeerenberg, *Berggren* 1868 (H). Seven Islands, *Berggren,* 1861 (H-SOL). Amsterdam Island, M. Bergren, 1861 (H-SOL). U.S.A. *Alaska:* Bering Sea, Hall Isl., *Trelease 2140* (MO). Franklin Mtns., NW of Mt. Chamberlin, *Steere 18707* (NY). Between Peters Lake & Schrader Lake, *Steere 18678* (NY). 0.8 mi. S of Jago Lake, *Cantlon & Gillis 57-1339D* (CANM). Pt. Barrow, *Steere 15113, 15103* (NY). Amchitka Isl., *Reich 1* (CANM). St. Attu Isl., N of Massacre Bay, *Jordal & Miller 3018* (BH). Lake Noluk, *Spetzmann M40* (US). Umiat area, Colville R., *Steere, Inoue & Iwatsuki 294* (NY). Endicott Mtns., Cascade Lake, *Steere 74-880* (NY). Cape Simpson, 50 mi. S of Barrow, *Steere & Iwatsuki 74-405* (NY). Driftwood Camp, Utukok R., Steere, *Martensson & Holmen 60-1059* (NY).

Pohlia andrewsii is characterized by its 1) leaves with a strong sheen when dry, and 2) its clusters of small, translucent, axillary propagula which have short, more or less rudimentary, or inconspicuous but often laminal leaf primordia. In the field, the propagula are difficult to see, because the erect leaves are generally imbricate and hide the inconspicuous, axillary clusters. Early in the growing season, the propagula are light, translucent-green, but rapidly become orange to orange-red with age. Young propagula have short, very inconspicuous leaf primordia, and these are generally incurved over the propagulum apex such that they sometimes appear absent, although they are consistently present (fig. 12: 1, 50: 10, 11, 13). Sometimes all the propagula of a given stem have these peglike primordia, but more frequently the primordium cells continue to divide and result in a small, laminal leaf primordium (fig. 50: 6). The laminal leaf primordia are also inconspicuous and difficult to see, being red-translucent like the propagulum body, and are incurved over the apex. In shape, the propagula are fairly uniform, varying from isodiametric to shortly oblong-linear (fig. 50), but do not become narrowly vermicular like those of *P. proligera* (e.g. fig. 62). Young propagula are nearly round (fig. 50: 2), sometimes becoming more elongate as a consequence of cell elongation in the propagulum body (fig. 50: 2). In general, lax, elongate stems growing in shaded rock crevices have longer propagula than compact stems growing in sunnier situations. In the field, *P. andrewsii* is usually easy to recognize because of its strongly translucent-red propagula which are well hidden by the leaves, and which appear to lack leaf primordia altogether under a hand lens. The length of the stem is sensitive to environmental factors and is, consequently, quite variable. The plants are sometimes only a few millimeters high, consisting of little more than a rosette of basal leaves, while at other times this species can grow to be three or four centimeters high, being one of the most robust propaguliferous species. The leaves have a distinct sheen when dry, and this character-state is uniform in the face of varying microclimate.

Specimens of *P. andrewsii* from arctic North America have mostly been confused with *P. annotina*, *P. proligera* and/or *P. bulbifera*. *Pohlia annotina* is a considerably more slender plant, and the leaves are dull green in contrast to the glossy leaves of *P. andrewsii*. The propagula of *P. annotina* are much more variable in shape (fig. 54), although its range of possible dimensions include types like those of *P. andrewsii*. Propagula of the latter species do not become so narrowly elongate as do those of *P. annotina* (e.g. fig. 54: 19, 20, 22), and they have not been observed to become large and bulbiform late in the season when occurring singly, as do those of *P. annotina*. Most importantly is the difference in the form and ontogeny of the leaf primordia. In *P. annotina*, the primordia are peglike, but are elongate and conspicuous (fig. 54), even on young propagula. Like *P. andrewsii*, the leaf primordia cells may later undergo cell division, becoming laminal in form (fig. 54). However, the laminal primordia are then large and erect, rather than small and incurved as are those of *P. andrewsii* (fig. 50: 17, 18, 19 versus fig. 54: 26). Only on the largest of *P. andrewsii* propagula, do the primordia appear erect (fig. 50: 23). Unlike *P. andrewsii*, the leaf primordia of *P. annotina* typically remain peglike, becoming laminal only on those propagula which remain attached to the stem for an unusually long amount of time. Most propagula of *P. andrewsii* produce laminal leaf primordia typically well before the end of a growing season. As herbarium specimens, the two are readily distinguished by the sheen of *P. andrewsii*, without even having to compare propagula. *Pohlia annotina* and *P. andrewsii* are compared quantitatively in figure 51. Note the greater morphological variability of *P. annotina*.

In gross appearance and particularly in leaf sheen, *P. andrewsii* is most similar to *P. proligera*, and these two species can only be confidently distinguished on the basis of propagulum morphology. The propagula of *P. proligera* are consistently narrowly vermicular, and not even the most elongate of *P. andrewsii* propagula approach them in form. Propagula of *P. proligera* most frequently have only a single leaf primordium (fig. 62), and it is always elongate and conspicuous relative to the propagulum body. In contrast, the primordia of *P. andrewsii* propagula arise as short proturberences, and commonly number (1)-2-4-(5). In herbarium specimens, the propagula of *P. proligera* appear as a dense, felty mass, while those of *P. andrewsii* appear as distinct clusters in each leaf axil.

Forms of *P. andrewsii* with isodiametric propagula may be confused with *P. bulbifera*, but the latter has leaf primordia which arise as laminal appendages (fig. 47). It is very infrequent that one finds a stem of *P. andrewsii* in which all the propagula have laminal primordia, and it is easy to demonstrate that they actually arise as peglike outgrowths (e.g. fig. 50). The laminal primordia of both species are incurved over the propagulum apex, but those of *P. bulbifera* are larger and considerably more conspicuous. Further, the propagula of *P. andrewsii* are strongly translucent and red, and contrast the green to orange, opaque or only slightly translucent propagula of *P. bulbifera*. When moist, the leaves of *P. bulbifera* are widespreading, and the propagula are easily visible under a hand lens. In contrast, as was noted above, the propagula of *P. andrewsii* are hidden by the erect leaves, and are difficult to see in the field.

The propagula of *P. camptotrachela* are similar to those of *P. andrewsii*, but are typically yellow or occasionally brown. Like those of *P. andrewsii*, the leaf primordia of *P. camptotrachela* arise as small, inconspicuous, peglike outgrowths, and are sometimes incurved over the propagulum apex (fig. 58). The primordia of *P. camptotrachela*, however, remain peglike and do not become laminal with age. The leaves of *P. camptotrachela* are dull, lacking any sheen, and as in *P. annotina*, this enables one to quickly distinguish it from *P. andrewsii*, without even looking at the propagula.

7. *Pohlia annotina* (Hedw.) Lindb., Musci Scand. 17. 1879.

Bryum annotinum Hedw., Spec. Musc. 183, 43. 1801. "Habitat locis arenosis argillosis, humidis, ad aggeres, fossas, aquas stagnantes continentes Germaniae." (Lectotype: G-Hedw.-Schwaegr. ! ["Olim Chemnitzii sax. lectum, no. 1"]).

Mnium annotinum (Hedw.) With., Syst. Arr. Brit. Pl. ed. 4, 3: 789. 1801.

Hypnum annotinum (Hedw.) Web. & Mohr, Ind. Mus. Pl. Crypt. 3: 1803.

Bryum decipiens Lam. & Cand., Fl. Franc. 2: 503. 1805. *nom. illeg. incl. spec. prior* (*B. annotinum* Hedw.).

Bryum bulbiferum Chev., Fl. Gen. Env. Paris 2: 75. 1827. *nom. illeg. incl. spec. prior* (*B. annotinum* Hedw.).

Webera annotina (Hedw.) Fuern., Flora 12 (Ergbl. 2): 35. 1829.

Pohlia grandflora H. Lindb., Medd. Soc. F. Fl. Fenn. 25: 41. 1900. Type: "Isthmus Karelicus, par Valkjärvi, 5 July, 1897, leg. H. Lindberg" (Lectotype: H!; Isotype: H!).

Webera proligera var. *tenella* Schiffner, Oesterr. Bot. Zeitschr. 51: 122. 1901. Type: "Madeira: Funchal, im curralinho, 600-700 m; ster. 22.III.1900 (sine Nr.)." (Lectotype:FH-Schiffn. !).

Webera corrensii Limpr. *ex* Loeske., Moosfl. Harz. 221. 1903. *nom. nud. in synon.*

Webera commutata var. *avimontana* Roth, Eur. Laubm. 2: 27. 1904. Type: "... 3 October 1896 an Waldwegen um den Taufstein im Vogelsberg in 750 m. ...." (Lectotype: S!).

Pohlia annotina var. *decipiens* Loeske, Verh. Bot. Ver. Brandenburg 46: 201. 1905. Type: "... zuerst Herr Torka aus der Umgebung vor Schwiebus und ... später in Eisenbahnausstichen bei Berlin ...." (Lectotype: B-Loeske! ["Berlin, Ausstich bei Sadowa" !]).

Webera annotina var. *decipiens* (Loeske) Roell, Hedwigia 46: 202. 1907.

Pohlia proligera var. *tenella* (Schiffn.) Herzog, Biblioth. Bot. 73: 17. 1910.

Webera grandiflora (H. Lindb.) C. Jens., Skand. Bladmfl. 259. 1939.

Webera grandflora var. *decipiens* (Loeske) Jans. & Wacht., Ned. Kruidk. Arch. 53: 215. 1943.

Webera stollei Warnst. *ex* Podp., Consp. 340. 1954. *nom nud.*

in synon.

Pohlia bulbifera var. *avimontana* (Roth) Warnst. *ex* Podp., Consp. 341. 1954.

Pohlia annotina var. *loeskei* Crum, Steere & Anderson, Bryologist 68: 434. 1965. (based on *Pohlia annotina* var. *decipiens* Loeske).

Plants slender, forming small, scattered populations or occasionally extensive turfs, dull-green and lacking a distinct sheen when dry; stems 4-10-(20) mm. high, green above, green to orange below, very rarely red just above the base, simple or sometimes once innovating at the base when sterile, simple when fertile; leaves erect-spreading to wide-spreading and sometimes with the lamina twisted and appearing somewhat caniculate when dry, erect-spreading to spreading when moist, (0.7)-0.8-1.1-(1.2) mm. long, 0.2-0.4 mm. wide, narrowly lanceolate to occasionally ovate-lanceolate, acute, shortly decurrent by 1-3 rows of linear to linear-rectangular cells, sometimes scarcely or not at all decurrent; margins plane, strongly toothed to subentire in the upper 1/2-1/3, entire to subentire below; costa ending 1-3 cells below the apex, green in young leaves, green or occasionally red-brown to red in older leaves, upper cells linear-rhombic to rectangular-rhombic, rarely vermicular, thin-walled, (35)-45-70-(105) um long, (6)-7-9-(11) um wide, variable in shape and size on a single leaf, undifferentiated at the margin, rectangular near the base, 3-6:1; asexual propagula usually present as clusters in the upper leaf axils of sterile shoots, sometimes appearing few, single or absent from old stems (often difficult to find on herbarium specimens), scarce or absent when fertile, arising in clusters in each upper leaf axil, extremely variable in size and shape, oblong, obconic to ± elongate and sub-linear, ± conspicuously tapered from apex to base, sometimes rounded-oblong and bulbiform when old, gradually narrowed to a uni- or biseriate stalk, mostly 150-300 um long, but occasionally only a few old propagula present (300-550 um long), the propagulum body and leaf primordia hyaline, yellow, green, orange or ± red when young, usually red when old and bulbiform, translucent, with (2)-3-5-(6) peglike leaf primordia present at the apex, sometimes becoming ± laminal on older propagula, arising as unicellular, fingerlike outgrowths, never as laminal appendages; perigonia bulbiform, terminal on unbranched stems, conspicuous; perigonial bracts long and narrowly acuminate from an ovate, concave, ± red-brown base; margins ± strongly toothed near the apex, toothed to subentire above the shoulders; costa filling the narrow acumen; perichaetia terminal, rather conspicuous; perichaetial bracts to ca. 3.3 mm. long, lanceolate to linear-lanceolate, often red at the base; costa ending just below the apex or in the apex; median cells on average, somewhat longer than those of the vegetative leaves, up to 115 um. long, sometimes ± incrassate; margins revolute from above the base to just below the apex, toothed in the upper 1/3. Dioicous; sporophytes occasional; seta 1.5-3.0 cm. long, orange-red to orange or orange-yellow; capsules positioned 95°-140° from the vertical, 2.0-3.0 mm. long, short to ± elongate pyriform, with a well developed neck which becomes ± shrunken when dry; exothecial cells longitudinally elongate and ± rectangular to irregularly isodiametric, 23-50 um long, 15-26 um wide, with strongly sinuose walls, especially when dry, less so when moist, gradually to abruptly smaller, less sinuose, sometimes thicker-walled and ± collenchymatous at the mouth, less sinuose and more nearly isodiametric in the neck, gradually elongate-rectangular just above the seta; stomata numerous in the neck, phaneropore, (30)-34-40-(46) um long; annuli well developed, of 2-(3) rows of cells, remaining attached to the urn or the operculum, sometimes separating irregularly or rarely ± revolvable; opercula conic and apiculate to occasionally umbonate; exostome teeth 16, yellow to yellow-brown above, often darker below, lanceolate, ± narrowly acute, coarsely papillose in the upper 1/3, more finely papillose below; endostome segments 16, hyaline, keeled, and broadly perforate; cilia (0)-1-3 between the segments, long, ± nodulose, sometimes short; spores baculate, (15)-18-23-(25) um.

Nomenclature: The nomenclature of *P. annotina* is discussed in detail in a previous section on the nomenclatural history of the propaguliferous complex. Dillenius (1741) described *Bryum annotinum lanceolatum pellucidum, capsulis oblongis pendulus,* and provided a plate illustrating the species (1741, fig. 68). According to Lindberg (1883), a specimen bearing this phrase in the herbarium of Dillenius is *Bryum pallens* (Brid.) Sw. *ex* Roell., and Dillenius' description and plate are consistent with that species. No mention of propagula was made in the *Historia muscorum,* and it seems clear that Dillenius did not use the epithet, *annotinum,* for any propaguliferous taxon. Linnaeus (1753) followed Dillenius on most bryological matters (Isoviita 1970), and he adopted Dillenius' (1741) diagnosis of *Bryum annotinum* ... almost without change (Linnaeus placed the species in *Mnium*). Like Dillenius, Linnaeus (1753) defined *Mnium annotinum* on the basis of the long-necked capsule and pellucid, lanceolate leaves. Schimper (1871) reported that a specimen marked *Mnium annotinum* in the Linnaean herbarium consists of two parts, one being *Ceratodon purpureus,* and the other *Bryum cernuum* (= *B. uliginosum* B.S.G.). The latter species is morphologically similar to *Bryum pallens,* the species to which Dillenius apparently applied the name *B. annotinum ...,* and it is likely that the inclusive "species" including these two taxa is what both Dillenius (1741) and Linnaeus (1753) intended with the epithet, *annotinum*. The inclusion of *Ceratodon* on Linnaeus' herbarium sheet is probably an inadvertant mixed collection since Linnaeus (1753) described that species elsewhere and a "correctly" named specimen exists in his herbarium (Schimper 1871). Most other botanists of the eighteenth century (e.g. Hudson 1762, Gunnerus 1772) used the name *Bryum* (or *Mnium*) *annotinum* without reference to propagula, following the phrase and plate provided by Dillenius (1741) and the description given by Linneaus (1753).

Leers (1775) described *Mnium annotinum*, including a discussion of its axillary propagula for the first time. Much discussion has been put forward as to which propaguliferous species Leers was actually referring, but none of his specimens are known (Sayre 1977), so it is impossible to know for sure how he applied the name. It is most likely that he used *M. annotinum* in an inclusive sense for several presently recognized taxa (see discussion in nomenclatural history section and Loeske 1907).

Hedwig (1801) provided the first description and illustration of *Bryum annotinum* which was sufficiently diagnostic to allow bryologists to associate the name with a definite, presently recognized species. His illustration (plate 43) shows both microscopic features and the species' habit, and includes detailed drawings of the propagula. The propagula are shown as small, obconic structures with several peglike, apical leaf primordia, the diagnostic features for recognizing this species. The propagula of *P. drummondii* and *P. filum* are much larger and branchlike, those of *P. proligera* are linear-vermicular and have only a single or two leaf primordia, and those of *P. andalusica* have broadly laminal leaf primordia. It is because of Hedwig's concise illustration that the epithet *annotina* has been used fairly consistently, at least in recent years.

Bryum annotinum Hedw. is represented by two specimens annotated by Hedwig in his herbarium in Geneva. Both specimens are interpreted by myself, Loeske (1905), and Ruthe (who annotated the specimens) as containing interspecific mixtures including *P. annotina, P. andalusica,* and *P. filum*. The first specimen ("*Olim Chemnitzii sax. lectum*") bears the page and plate citations from *Species Muscorum* and contains three samples of *P. annotina,* three of *P. andalusica,* two of *P. annotina* and *P. andalusica* mixed, and five of what appear to be perigonial plants of *P. filum* (see section on nomenclatural history). The second specimen has no collection locality given but lists *Bryum annotinum* Dill., *Mnium annotinum* L., and *Trentepohlia erecta* A. Roth as synonyms. This specimen is interpreted as containing eight samples of *P. annotina,* and one of

P. andalusica.

Article 70 of the ICBN allows that a portion from a herbarium sheet containing discordant elements may be selected to lectotypify a name when only one element is consistent with the protoloque of the original publication. As was stated above, Hedwig's (1801) plate 43 can be associated with only one presently understood species, and therefore I suggest that the shoots marked no. 1 on the sheet bearing the notation *"Olim Chemnitzii sax. lectum"* be considered lectotype.

During the nineteenth century, with the exception of *Webera gracilis*, no new propaguliferous species (of this group) were described until Schimper (1876) published *Webera commutata* (*Bryum drummondii* C. Müll. 1862 was not recognized as a propaguliferous species until Andrews (1935) made the new combination in *Pohlia*). Thus, when Lindberg studied the group in the 1870's, only *P. filum* (as *Webera gracilis*) and *P. annotina* were known to science. In 1871, Lindberg proposed the new genus *Lamprophyllum (nomen nudum)*, and made the combination *L. annotinum* (Hedw.) Lindb. In his *Musci Scandinavici*, Lindberg (1879) transferred this species to the genus *Pohlia*, again publishing a new combination, *P. annotina* (Hedw.) Lindb. It is well known that Lindberg never accepted Hedwig (1801) as the nomenclatural starting point for *Musci*, and consequently in 1879 he cited Linnaeus as the basionym author in his new combination. This was an unfortunate decision on Lindberg's part since eight years previously, Schimper (1871) had reported that Linnaeus' "type" specimen of that name was not even a *Pohlia*. The code does allow that by designating Hedwig (1801) as the nomenclatural starting point, Lindberg's (1879) reference to Linnaeus (1753) could automatically be changed to Hedwig (1801) when citing the species. On the other hand, as was pointed out by Isoviita (in litt.), the correct interpretation of Lindberg's nomenclatural practice is probably more important in this case. The important question is whether Lindberg intended to publish a new species in 1871 and 1879, excluding the type of *Bryum annotinum* Hedw., or whether he simply intended new combinations for Hedwig's species, referring only to Linnaeus for the sake of brevity. If it is concluded that Lindberg meant to publish a new species, then the code requires that the name *Lamprophyllum annotinum* be typified independently of Hedwig's earlier *Bryum annotinum*. However, if it is concluded that Lindberg did not implicitly exclude the type of *Bryum annotinum* Hedw. (it was not explicitly excluded), then there seems to be no rule which denies the possibility of typifying Lindberg's combinations with Hedwig's specimens, even though Hedwig was not actually referred to. There is convincing evidence from Lindberg's other publications and from the notations on his specimens in H-SOL, that he included both *P. andalusica* and

P. annotina, as well as *P. bulbifera* and *P. filum* in his application of the name *Pohlia annotina* (see pages for detailed discussion). Although some recent authors (e.g. Buch 1906, Koch 1951, Lewis & Smith 1978) have argued that Lindberg applied the name *P. annotina* exclusively to the plant presently known as *P. andalusica*, I cannot agree with that opinion because of the facts given on pages 91-94. Given that Lindberg implicitly included Hedwig's type in *P. annotina* (1879), I think it is best to accept his combination, citing the name as *P. annotina* (Hedw.) Lindb.

In 1900, H. Lindberg published the name *P. grandiflora* H. Lindb. for Hedwig's species, being of the opinion that his father had used *P. annotina* exclusively for *P. andalusica*. This was probably based on an examination of his father's specimens so-named from around Helsinki, which are mostly *P. andalusica*. However, by studying the whole of S.O. Lindberg's collection named *P. annotina*, it is clear that Lindberg did not distinguish these species (see pages 91-94.

During the present century, opinions have varied concerning the nomenclature of *P. annotina*. Nyholm (1958), Crum, Steere and Anderson (1973), Margadant (1968), Gradstein (1971) and Steere (1978) have accepted Lindberg's combination, citing the plant as *P. annotina* (Hedw.) Lindb., while Koch (1951), Wilczek and Demaret (1970) and

Lewis and Smith (1978) have rejected *Pohlia annotina*, adopting a later name which they thought appropriate.

Distribution: (fig. 52). The North American distribution of *P. annotina* is bicentric, with one center in eastern United States and the other along the Pacific coast of Canada and northwestern United States. In the eastern part of the continent it extends considerably farther south than any other propaguliferous species, reaching Georgia and Arkansas. It occurs occasionally (probably under-collected) along thh eastern states, collections being particularly frequent in northern New York, New England, and into Newfoundland. A few outlying populations have been collected westward to Wisconsin, Missouri and Iowa. In the western portion of its distribution, *P. annotina* has been collected from southern Washington northward along the coast of British Columbia to southern Alaska. Specimens have been examined from scattered localities along the Aleutian chain, and Ochi (1959) reported the species from Japan (as *P. camptotrachela*). *Pohlia annotina* is known from several localities in the interior (Selkirk) mountains of British Columbia, but has been collected only once in the Canadian Rockies (Mt. Robson, B.C.). It is known from two localities in Montana but all reports of this species in the central Rocky Mountains are referrable to *P. tundrae* or *P. camptotrachela*. *Pohlia annotina* is not known from arctic North America, and all reports from northern Alaska, the Yukon Territory and Northwest Territories are referrable to *P. andrewsii*. Non North American specimens have been examined from Austria, Belgium, Crete, Czechoslovakia, Denmark, East Germany, England, Faroe Islands, Federal Republic of Germany, Finland, France, Ireland, Italy, Netherlands, Poland, Sweden and Turkey. Preliminary data indicate than in and around Europe, like in North America, *P. annotina* extends farther south than any other propaguliferous species, reaching Crete and Turkey. In Africa, *P. baronii* Wijk. & Marg. has propagula very similar to *P. annotina*, but the plants are more highly branched and it may well be a good species (see also, the similar opinion of Demaret & Wilczek 1977).

Selected Specimens Examined: Exsiccati. Andrews (1935) cited Sullivant and Lesquereux's exsiccati no. 171 (ed. 2) as *Pohlia rothii*. The duplicates which I have examined (BH, MICH) both contain two different elements on the same sheet. Within a small packet is typical *P. annotina* (with propagula), but mounted separately are samples of *P. drummondii* (mostly with sporophytes, but propagula seen - BH!). Sull. & Lesq., no. 180 (ed. 1), also as *B. annotinum*, is *P. drummondii* and the plants agree closely with that species on no. 171. Quite possibly they came from the same collection ("in Novae Angliae Montosis"). However, the collection must have been a mixed one, for no. 180 in MICH is *P. bulbifera*. See under *P. proligera* (specimens examined) for further discussion of several problematic exsiccati numbers.

North America: Allen, Mosses of the Cascade Mtns. 54 as *P. proligera* (COLO, MICH, MO, NY, UBC, US - all in part); Austin, Musci Apal. 188 as *B. annotinum* (US, CAS); Grout, North Am. Musci Perf. 291 as *P. annotina* (BH, CAS, COLO, F, MICH, MIN, SMU, TENN, US); Holzinger, Musci Acr. Bor.-Amer. 12 as *P. proligera* (MIN); 45 as *P. proligera* (MIN); 394 as *W. annotina* (CANM, COLO, MICH, MIN, MO, US); 450 as *W. proligera* (BH, CANM, COLO, H, MICH, MO, NY); 662 as *P. grandiflora* (BH, CANM, COLO, MICH, MIN, MO, US, WIS); Macoun , Can. Musci 464 as *W. annotina* (CANM, MICH, MO, NY, US); 448 as *W. annotina* (WTU, US); 438 as *W. microsporum* (US); 162 as *W. annotina* (WIS), NY - in part); Macoun, Can. Mosses 463 as *W. proligera* (NY, MICH, MO, US); Sull. & Lesq., Musci Bor. - Amer. (ed. 2) 171 as *B. annotinum* (NYS, BH, MICH, MIN). Europe: Bauer, Musci Eur. Exs. 309 as *P. annotina* (BH, ALTA, F, COLO); 1621 as *P. annotina* (ALTA, WTU, COLO); 1622 as *P. annotina* var. *decipiens* (ALTA, COLO); 1090 as *P. annotina* f. *decipiens* (F, COLO); Cryptogamae Exs. 3771 as *W. annotina* (UC - completely; MO, US, COLO - all in part); Holmen, Bryoph. Danica Exs. 426 as *W. annotina* (ALTA, CAS, COLO, US); Husnot, Musci Galliae 769 as *W. annotina* (BH, WIS); Kopsch, Bryoth. Sax. 241 as *P. proligera* (MICH); 242 as *P. grandiflora* (MICH); 335 as *P. grandiflora* (MICH, H); 420 as *P. grandflora* f. *decipiens* (MICH); Lisowski, Bryoth. Polonica 484 as *P. grandiflora* (CANM, H); Mickiewicz, Plantae Vars. Exs. 56 as *P. grandiflora* (CANM, H); Rabenhorst, Bryoth. Eur. 968 as *B. annotinum* (H-SOL, UC); Roze & Besch., Musc. des Environs de Paris 186 as *W. annotina* (CANM); Warnstorf, Mark. Laub. 174 as *W. annotina* (CAS).

Canada. *British Columbia:* Revelstoke area, 14.5 mi. (1 mi=1.6 km) S of Revelstoke at Blanket Cr. Cmgd., *Vitt 22388* (ALTA). Queen Charlotte Islands, Graham Isl., just N of Pure Lake, *Horton 1781* (ALTA). East of Vançouver, 3 mi. W of Alder Grove, *Vitt 4628* (ALTA). Prince Rupert area, along Oldfield Cr., *Shaw 1580* (ALTA). Glacier Nat. P., along Avanlanche Crest Trail, *Shaw 2154* (ALTA). Nakusp area, 22.0 km N of Nakusp on Hwy. 23, *Shaw 2208* (ALTA). Mt. Robson area, Berg Lake Trail, *Shaw 2834* (ALTA). *New Brunswick:* Charlotte Co., 3 mi. N of Digdequash, *Ireland 17034* (CANM). York Co., 3 mi. N of Lake George, *Ireland 12986* (CANM). Albert Co., Fundy Nat. P., *Ireland 11536* (CANM). *Newfoundland:* Wesleyville area, 3 km. WNW of Cape Freels North, *Belland 270* (NFLD). Woodstock, 49°58'N, 55°53'W, *Brassard 11259* (NFLD). Lance Cove, *Belland & Brassard 12170* (NFLD). Aquaforte, Ferryland, *Tuomikoski 572* (H). *Nova Scotia:* Shelbourne Co., 3 mi. N of Upper Clyde R., *Ireland 12373* (CANM). Cumberland Co., 2 mi. N of Advocate Harbor, *Ireland 17271* (CANM). Halifax Co., 3 mi. E of Musquodoboit, *Ireland 12139* (CANM). *Ontario:* Dorchester Copper Mines, *Beschel 22* (COLO). Algoma district, between Agawa Bay & Montreal River, *Sharp CM601* (DUKE). Renfrew Co., 3 mi. N of Brudenell, *Ireland 15858* (CANM). *Quebec:* Magdalen Island, *Reilly 961* (MICH). Waterloo, *Anselm 1356* (WIS). Gaspe, Forillon Park, *Shaw 681* (Priv. Herb. J. Shaw). U.S.A. *Alaska:* Ketchikan area, ca. 5 mi. N of Ketchikan at Ward Lake cmgd., *Shaw 1633* (ALTA). Juneau area, along dirt road on NE side of Maginnis Mtn., *Shaw 2019* (ALTA). Middleton Island, near airforce base, *Thomas 5952a* (CANM). *Arkansas:* Washington Co., E of Springdale, *Anderson 21345* (DUKE). *Georgia:* Dekalb Co., N slope of Stone Mtn., *Small*, 1893 (BH). Macon Co., near summit of Rabun Bald, *Steere 10165* (MICH). *Idaho:* Salmon Nat. For., Gibbonsville area, *Shaw 2714* (ALTA). Shoshone Co., 9 mi. northeast of Wallace, *Hermann 22560* (US). *Iowa:* Winneshick Co., E of Hesper, *Conard 7-104* (TENN). *Maine:* Mt. Katadin, near Baxter camp, *Andrews*, 1950 (BH). Cumberland Co., Congress St. in Portland, *Pilman 9636* (BH). Piscataquis Co., 13 1/2 mi. N of Milo, *Hermann 19161 1/2* (US). *Maryland:* Prince George Co., 2 mi. W of Beltsville, *Hermann 15857* (US). *Massachusetts:* Mt. Greylock, *Andrews*, 1910 (BH). Brewster, *Andrews*, 1936 (BH). Amesbury area, *Huntington*, 1901 (BH). *Michigan:* Cheboygan Co., N of Douglas Lake, *Miller 3386*

(MICH). Alger Co., Pictured Rocks near Miner's Castle, *Miller 2721* (MICH). Keweenaw Co., 1 mi. W of Lac La Belle, *Hermann 23139* (MICH). *Missouri:* St. Clair Co., 4.5 mi. E of Osceola, *Redfearn & Weber 27369* (SMS). Cedar Co., 6 mi. SE of Stockton, *Redfearn 12829* (US). *Montana:* Lincoln Co., Cabinet Mtns., *Flowers*, 1967 (COLO). Missoula Co., banks of Lolo Nat. For. Rd. 905, *Shaw 2721* (ALTA). *New Hampshire:* Camp Duncan, Bretton Woods, *Smith & Miller 34128* (NYS). White Mtns., vicinity of Mt. Washington, *Miller 1655* (NYS). Grafton Co., Bright Hollow, *Hutchinson 3* (BH). *New York:* Staten Island, *Grout*, 1931 (DUKE). Tompkins Co., Homers Gulf, *Andrews, Muenscher & Nanz*, 1920 (BH). Rensselaer Co., 1 mi. E of Poestenkill, *Smith & Carr 35000* (NYS). Suffolk Co., Sagaponack, *Latham 33965* (NYS). Livingston Co., Letchworth State Park, *Miller 1697* (NYS). *North Carolina:* Dark Ridge, *Andrews 360* (BH). Winston Salem, *Schallert 5* (BH). *Ohio:* Hocking Co., Hocking Hills St. P., *Forman 621* (MICH). Jackson Co., Jackson, *Bartley 538* (US). *Pennsylvania:* Shroudsburg, *Chapman 2427* (BH). Montgomery Co., Willow Grove, *Pinckney*, 1972 (US). Deleware Co., Swarthmore, *Cresson*, 1904 (BH). Sevier Co., Sugarland Valley, *Sharp 4577* (TENN). *Vermont:* Mt. Horrid Region, *Andrews*, 1947 (BH). Stratton Mtn., *Sharp*, 1932 (DUKE). Rutland Co., Meddletown Springs, *Carpenter*, 1917 (BH). Windsor Co., 10 mi. N of Windsor, *Miller 7919* (FH). *Virginia:* Nansemond Co., 7 mi. NE of

Cypress, *Ireland 4053* (US). Henrico Co., Richmond, *Gatterson 1031* (WIS). *Washington:* Mt. Baker area, ca. 5 mi. SE of Mt. Baker on rd. 385, *Shaw 2304* (ALTA). Snohomish Co., Mt. Loop Hwy., 0.25 mi. N of Barlow Pass, *Shaw 2326* (ALTA). Jefferson Co., Olympic Nat. Park, *Shaw 2389* (ALTA). Pierce Co., Mt. Rainier area, *Frye*, 1923 (WTU). *West Virginia:* Monongaha Co., Lick Run, *Andrews*, 1903-04 (BH). *Wisconsin:* Marathon Co., *Freckman 1009* (MICH).

Pohlia annotina may be characterized by its 1) slender habit and nonglossy leaves, wet or dry, and 2) clusters of variably shaped axillary propagula having 2-4-(6) apical leaf primordia arising as peglike outgrowths. The color, shape and size of the propagula are almost incredibly variable in this species. They are distinctly and consistently translucent, but may be whitish, hyaline, yellow, orange, red, or occasionally pale-green. Very long, narrow propagula tend to be palest, often appearing white or almost hyaline. Large, solitary, bulbiform propagula are most often translucent-red, but may vary to many shades of orange. Typical, shortly obconic forms (cf. Hedwig 1801, plate 43) tend to be orange or red, but sometimes green or yellow forms are encountered. Consequently, propagulum color alone is of little value in recognizing this species. The propagula are no less variable in shape than in color (fig. 54), ranging continuously from shortly ovate or obconic (fig. 54: 1-9) to linear and scarcely tapered to the base (fig. 54: 22). Much morphological variation occurs developmentally, and because a single stem continuously produces propagula in each leaf axil, a considerable range of forms may be encountered from one plant at one point in time. Early in their ontogeny, (1)-2-4 peglike leaf primordia are differentiated from the propagulum body as elongate, fingerlike outgrowths (fig. 54: 1-10). As the growing season progresses, the propagula produced early on continue to grow in size and complexity, even while attached to the stem, invariably producing at least two peglike primordia (fig. 54: 21, 25), and more commonly three or four (fig. 54). When only one or two primordia are present, it is usually possible to find a young primordial initial near the propagulum apex beginning to elongate to form additional primordia (fig. 54: 12). Depending upon the degree of longitudinal elongation of the body cells, the propagulum may become long and narrow (fig. 54: 19, 22); Lewis & Smith 1977, type F), shortly obconic (fig. 54: 13, 15, 16; Lewis & Smith 1977, type D), or any one of an infinite number of possible intermediate forms (fig. 54: 10-12; Lewis & Smith 1977, type E). The ontogeny of the propagula, particularly with respect to the degree of cellular elongation, must be sensitive to microenvironmental variation, and is plastic in ontogenetic response. Light intensity and possibly light quality (Hoddinodd & Bain 1978) could be important factors controlling development. Schmalhausen (1949) labelled this kind of environmentallly controlled, morphologically plastic development, dependent morphogenesis, and discussed its importance as an adaption to short term, unpredictable, environmental variation. Bradshaw (1965) discussed phenotypic plasticity in plants as an evolutionary adaption, and suggested that high plasticity may be considered an alternative to the maintenance of high levels of genetic variability. The indeterminate nature of propagulum growth while attached to the parent stem allows for continuous developmental modification in response to a rapidly changing micro-environment.

Although some variation, other than developmental, exists in a single population, for the most part a given population has either long narrow propagula, shortly obconic propagula, or intermediate types, etc., and extremes along this continuous morphological gradient are rarely encountered in close proximity. This could be the result of relative genetic homogeneity within populations with some differentiation between them, as would be expected in a plant whose breeding system consists of short range, frequent vegetative reproduction and occasional dispersal of sexual propagules. It is likely that any given "population" of *P. annotina* represents a single, or a few genotypes extensively reproduced asexually. Lewis and Smith (1977) showed that there is considerable genetic variation between populations with respect to propagulum length-width ratios in the British Isles, and that this genetic differentiation is superimposed on extensive phenotypic plasticity, the result being a continuous gradient of propagulum shape (fig. 54).

While the long, narrow types of propagula (fig. 54: 19, 22) are characterized by extensive cellular elongation, they are generally only 3-6 cells in diameter. On the other hand, in forms in which the body cells remain isodiametric (fig. 54: 23, 24) or nearly so (fig. 54: 14), the propagulum often becomes considerably thicker by cell division, often consisting of 8-15 cells in diameter. During ontogeny, the leaf primordia produced early on cease development, remaining as uni- or sometimes bi- (or tri-) cellular outgrowths (fig. 54: 1-22), although additional primordia may be produced in a spiral sequence by elongation of cells near the apex (fig. 54, and Correns 1899). On propagula which remain attached to the stem late in a growing season, and become large, and bulbiform (fig. 54: 26), the leaf primordia may become 2-4-(6) cells broad at the base, assuming a truly laminal form. In these cases, however, the primordia arise as peglike outgrowths (fig. 54: 14), and their laminal form is of a secondary nature, in contrast to e.g. *P. andalusica*, where even young propagula have broadly laminal leaf primordia (fig. 40: 1). From European herbarium material, I have found that the very large, bulbiform propagula (e.g. fig. 54: 23-26) are occasionally encountered in the lower leaf axils of plants collected late in a growing season (see also Lewis and Smith 1977, 1978). However, I have never encountered these extreme expressions from North American material, either in the field or as herbarium specimens, and it is possible that North American populations are less variable in this respect. Forms illustrated in figures 54: 1-22 represent the observed range of variation on this continent, but I have included figures 54: 23-26, since such types may eventually be encountered by collectors. In all other respects, European specimens of *P. annotina* are indistinguishable from their North American counterparts, and exhibit all the variation present in our material and then some.

Because of the continuous nature of propagulum shape discussed above, I have been unable to consistently recognize a variety *decipiens* Loeske within *P. annotina*. Although when encountered, the very long, narrow forms of propagula are distinctive, intermediate types are far more frequent. I have not been able to document any ecological or geographic differences between the extremes along this morphological gradient, and consequently *P. annotina* var. *decipiens* is herein treated as a synonym of the species.

The outstanding variation inherent in the propagula of *P. annotina* make this species difficult to identify. There are, however, a few critical features which are sufficiently uniform within the species to allow its unambiguous definition and identification. Without even studying the propagula, the slender habit and especially the dull, glossless leaves distinguish *P. annotina* from all other North American propaguliferous species except *P. camptotrachela*. Further, whatever the shape or size of the propagula, they consistently have 2-4-(6) apical leaf primordia which arise as elongate, fingerlike outgrowths. Even on plants in which the propagulum leaf primordia have become more or less laminal in form (fig. 54: 23, 24), it can be demonstrated on other propagula of the stem, if not on the same propagulum, that they begin as peglike outgrowths (fig. 54: 1-14).

Pohlia annotina has been confused by North American bryologists with *P. camptotrachela, P. andrewsii, P. proligera,* and *P. tundrae*. See under *P. camptotrachela* for the features distinguishing that species from *P. annotina,* and under *P. andrewsii* and *P. tundrae* for distinctions between these pairs of species.

Pohlia proligera has sometimes been confused with forms of *P. annotina* in which the propagula are narrowly linear (e.g. fig. 54: 10, 22). However, as was noted by Crum (1976), the two species are readily distinguished by differences in habit and leaf sheen. For the most part, *P. proligera* is more robust, and the leaves are conspicuously glossy when dry. When moist, the leaves of *P. proligera* are commonly more erect and imbricate, and they often hide the axillary propagula unless pushed aside. *Pohlia annotina* has more spreading leaves, and the propagula are more readily visible, even in forms in which the propagula are shortly obconic. When *P. annotina* has long, narrow propagula, these generally extend widely from the stem, and are obvious under a hand lens in the field. The propagula of *P. proligera* are strongly vermicular, and form a tight, almost felty mass within the upper leaf axils; it is often difficult to distinguish the separate clusters in each leaf axil. They are dislodged from the stem less readily than those of *P. annotina,* and most frequently the mass of propagula remain intact on herbarium collections. *Pohlia annotina,* on the other hand, has the propagula less densely massed together, and the individual propagula appear coarser, broader and more distinct. Specimens of *P. annotina* have frequently lost their propagula altogether after being dried. When dry, stems of *P. annotina* often have their leaves in various flexuose and curled positions, frequently twisted longitudinally and appearing very narrow, although sometimes they are stiffer and hardly modified from the moist condition. Those of *P. proligera* are consistently less contorted when dry, sometimes being more or less flexuose near the apex.

In details of ontogeny and morphology, the propagula of these species differ consistently. Those of *P. proligera* are narrowly linear-vermicular, do not become oblong or bulbiform at any stage of growth, and the propagulum body cells are always more or less elongate-rectangular to linear (fig. 62). The leaf primordia most frequently arise as single, peglike outgrowths, and are often characteristically bent at an angle from the propagulum body (fig. 62). Some propagula on most *P. proligera* stems produce two leaf primordia, but three or more have never been observed in this species (fig. 62), and they do not become laminal at any stage of development. In contrast, the propagula of *P. annotina* have 3-4-(6) leaf primordia, and these are erect from the propagulum body. As discussed above, propagula of *P. annotina* continue growth while attached to the stem, becoming larger, sometimes longer, sometimes more oblong and bulbiform, and usually continuing to produce leaf primordia. Some *P. annotina* stems which produce long, narrow propagula have "immature" stages which have only one or two primordia, and appear similar to those of *P. proligera* (fig. 54: 21). Almost invariably, however, typical older propagula with 3-4 primordia are also present on the same stem, and usually the initial cell later to produce a third primordium can be seen on the young propagulum with only two primordia (fig. 54: 21). Although the earliest ontogenetic stages of the propagula are sometimes similar in *P. proligera* and *P. annotina*, those of the latter species are more indeterminate in their growth than those of the former. This similarity in early ontogeny is to be expected between two homologous structures (see also pp. 48-52). *Pohlia proligera* and *P. annotina* are compared quantitatively in figure 55. Note the greater spread of points in *P. annotina*, this reflecting its variable morphology and indeterminate growth. The type of *P. proligera* var. *tenella* Schiffn. is a form with dull leaves as in *P. annotina*, but which has clustered propagula which seem to have been abnormally arrested in their development as a stage corresponding to those of *P. proligera*.

Loeske (1906) discussed the relation between his variety *decipiens* (long, narrow propagula) and *P. proligera*. He pointed out that forms of *P. annotina* with slender propagula are also lax and slender in general habit, differing even more from *P. proligera* in habit than do typical expressions of *P. annotina*. He went on to argue that if *P. annotina* var. *decipiens* (sic) were actually intermediate between the species and *P. proligera*, one would expect it to converge in all features, and not only in propagulum length-width ratios. I quite agree with Loeske's reasoning.

Although the propagula are far more variable in *P. annotina* than in *P. proligera*, this is not so for all features of the two species. The perigonial bracts of *P. annotina* are always longly acuminate from the ovate base, and display little variation in this feature (fig. 53:

17, 18). Those of *P. proligera,* on the other hand, may vary from shortly acute to longly acuminate, and are apparently subject to considerable environmental modification (fig. 61: 16, 17). Plants of *P. proligera* growing in shaded habitats tend to have longly acuminate bracts, while those in sunnier localities have shortly acute bracts (see also pp.

That *P. proligera* and *P. annotina* have quite different geographic distributions in North America (fig. 52, 60), indicates that these morphologically defined species have definite, individual, biological meaning. Further, the two differ significantly along the gradient of substrate pH, and do not frequently coexist in the same habitat (see pp.

8. *Pohlia camptotrachela* (Ren. & Card.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 552. 1903.

Webera camptotrachela Ren. & Card., Bot Gaz. 13(8): 199. 1888. also: Bull. de la Soc. bot. Belg. 27(1): 1888. Type: "California, a cl. Lesquereux communicata" (Isotype: NY!).

Bryum nutans ssp. *camptotrachelum* (Ren. & Card.) Kindb., Eur. N. Am. Bryin. 2: 385. 1897.

Bryum camptotrachelum (Ren. & Card.) Paris, Ind. Bryol. Suppl. 59. 1900.

Plants slender, forming small to extensive turfs, sometimes intermixed with other mosses, dull, often dark-green and somewhat stiff in appearance when dry; stems 5-15 mm. high, green above, green or sometimes ± red near the base, simple or occasionally once innovating at the base when sterile, simple when fertile; leaves spreading to erect-spreading and sometimes ± flexuose when dry, spreading to erect-spreading when moist, (0.6)-0.8-1.1-(1.4) mm. long, (0.2)-0.3-0.5 mm. wide, narrowly to broadly lanceolate, acute, nondecurrent or ± decurrent by 1-3 linear-rhombic cells; margins plane, strongly toothed to subentire in the upper 1/3, entire to subentire below; costa ending 1-3 cells below the apex, green in young leaves, green or sometimes ± red or brown near the base in older leaves; upper cells rectangular or rhombic to ± linear-rhombic, sometimes vermicular, thin walled, (40)-50-75-(100) um long, (6)-7-10-(11) um wide, variable in size and shape on a single leaf, undifferentiated near the margin, rectangular near the base, 3-6:1; asexual propagula usually abundant as dense, axillary clusters in the upper leaf axils of sterile shoots, sometimes scarce on old shoots (often difficult to find in herbarium specimens), scarce or absent from fertile plants, rather uniform in shape and size, globose to slightly elongate but rarely more than twice as long as wide, never elongate and narrowly vermicular, ± abruptly narrowed to a uni-(bi)seriate stalk, mostly 70-120-(175) um in the longest dimension, rather uniform in color, typically yellow, but occasionally brown, especially older propagula, translucent, with 1-3-(5) short, peglike leaf primordia present at the apex, the primordia arising as short, peglike outgrowths, never as laminal appendages, sometimes poorly developed, often incurved over the propagulum apex; perigonia bulbiform, terminal on unbranched stems, conspicuous; perigonial bracts long and narrowly acuminate from an ovate, concave, ± red-brown base; margins ± strongly toothed near the apex; costa filling the acumen; perichaetia terminal on unbranched stems, ± conspicuous; perichaetial bracts to ca. 3.0 mm. long, lanceolate to linear-lanceolate, sometimes ± red at the base; costa strong, ending in the apex or 1-3 cells below; median cells, on average, somewhat longer than those of the vegetative leaves, often ± incrassate, to 110 um long; margins revolute from above the base to just below the apex, toothed in the upper 1/3. Dioicous; sporophytes rather frequent in montane (but not alpine) habitats; seta 1.5-3.0 cm. long, orange to orange-red; capsules positioned 95°-145° from the vertical, 2.0-3.0 mm. long, short to ± elongate pyriform, often abruptly contracted to the well developed neck when dry; exothecial cells longitudinally elongate and ± rectangular to irregularly isodiametric, 28-42 um long, 13-34 um wide, with strongly sinuose walls, especially when dry, less so when moist, gradually to ± abruptly smaller, less sinuose, and thicker walled near the mouth, less sinuose and more nearly isodiametric in the neck, gradually to abruptly elongate-rectangular just above the seta; stomata numerous in the neck, phaneropore, (35)-45-53-(60) um long; annuli well developed, of 2-(3) rows of cells, remaining attached to the urn or the operculum, sometimes separating irregularly or rarely ± revolvable; opercula conic and usually apiculate; exostome teeth 16, yellow to yellow-brown above, sometimes darker below, lanceolate, ± narrowly acute, coarsely papillose in the upper 1/3, more finely papillose below; endostome segments 16, hyaline, keeled, and broadly perforate; cilia (0)-1-3 between the segments, long, ± nodulose, sometimes short; spores bacculate to clavate, 13-17-(21) um.

Nomenclature: *Pohlia camptotrachela* was described (as *Webera*) from California by Renauld and Cardot in 1886. The name was also published in the Bulletin de la Société botanique de Belgique (27(1): 1886) in French, so that, according to the authors, it would also be more accessible to European bryologists. After being described in 1886, *P. camptotrachela* was placed in synonymy of *P. annotina* (Hedw.) Lindb. by Andrews (1935). Later, Koch (1951) suggested the name *P. camptotrachela* as a replacement for *P. annotina*, which he considered a *nomen ambiguum*. On the basis of culture studies, Lewis and Smith (1977, 1978) reported that *P. camptotrachela* is a species distinct from *P. annotina*, and confirmed its occurrence in the British Isles. My own herbarium and culture studies are in agreement with the conclusion arrived at by Lewis and Smith, and *P. camptotrachela* is considered here as distinct from *P. annotina*, both of which occur in North America.

The isotype examined from NY is a notably depauperate specimen consisting of a few stems with sporophytes and with some loose propagula within the herbarium packet. These propagula are somewhat more elongate than is typical for the species, and approach those of *P. annotina* in shape. The latter species, however, is not known to occur in California, so the type cited by Renauld and Cardot can be confidently considered to represent *P. camptotrachela*. Unfortunately, a specimen from the Cardot herbarium (presumably in PC) has not been made available to me, so I have chosen not to lectotypify *P. camptotrachela* at present.

In the protologue of *P. camptotrachela*, Renauld and Cardot distinguished their new species from *P. annotina* by its longer, more curved capsule, and its reduced endostome. I find neither of these features to be consistently diagnostic for *P. camptotrachela*, which is distinguishable from *P. annotina* solely on the basis of its propagula (see below). Both *P. annotina* and *P. camptotrachela* sometimes have capsules with well developed necks almost equal in length to the urn, resembling those of e.g. *P. nutans* (but not so orange). I suspect that the reduced endostome observed by Renauld and Cardot was an artifact resulting from damage while collecting the plants.

Distribution: (fig. 54). In North America, *P. camptotrachela* is distributed widely in the mountains of western United States and British Columbia. Collections have been examined from California (Inyo Co.) northward in the Pacific coast mountains to Port Moody, British Columbia. In the Rocky Mountains, *P. camptotrachela* is known from Colorado (Boulder Co.) northward to Revelstoke, British Columbia, in the Selkirk Range. Non North American specimens have been examined from England, France, Germany, and Scotland, and Lewis & Smith (1978) reported this species from Sweden.

Selected Specimens Examined: Exsiccati. Europe: Bauer, Musci Acro. Bor. Am. 450 as *P. proligera* (MIN); 904 as *P. annotina* (COLO); Mickiewicz Plantae Vars. Exs. 56 as *P. grandiflora* (BH). Canada. *British Columbia:* Revelstoke Area, *Shaw 2818* (ALTA). Creston Area, 300 ft. S of Kootenay Pass on Hwy. #3, *Shaw 2744* (ALTA). Kokanee Glacier Prov. P., Esmerelda Cr. Trail, *Shaw 2775* (ALTA). U.S.A. *California:* Inyo Co., Mammoth Lakes Area, *Weber B-34768* (COLO). Duck Lake, *Koch & Koch 2215a* (with *P. proligera*) (MICH). Tuolumne Co., Sonora Pass Rd, Niagra

Cr. Cmgd., *I.L. Wiggins 8977* (COLO), *MacFadden 21846* (CANM), 10 mi. (1 mi. = 1.6 km.) E of Longbarn on Hwy. 108, *Koch 2193* (MICH). Smocky Jack Cmgd., Tioga Pass Hwy., *Koch 1744* (MICH). Near Sonora Pass, *Howell H-118* (CAS). Yosemite Nat. P., Vernal Falls Trail, *MacFadden 17454* (COLO). On Big Oak Flat Rd., *I.L. Wiggins C-53* (UBC). Yosemite Valley, *Mulik 8082* (COLO). Plumas Co.: Bucks Ranch, springy ground, *J.B. Leiburg 5443* (BH). San Bernadino Mountains, North Side of Bear Lake, 6900 ft., *Muzz 5736* (BH). Nuada Co., Summit of Donner Lake. *MacFadden 9020* (BH). Placer Co., Near Haig Tree in Big Tree Grove, *Koch 3155* (CANM). Berkeley, near Claremont Hotel, *E. Morse 28* (UC). Siskiyou Co., Mt. Shasta, *Koch 15657C, 15706D* (UC). Dunsmuir, *D. Richards & F. Drouet 1275* (MICH). Shasta Co., near Hat Lake, Lassen Nat. P., *Koch 1927* (MICH). Nevado Co., Carr Lake, *Koch 2020a* (MICH). Calaveras Co., 1 mi. N of Avery. *W. Wagner 4356* (MICH). Eldorado Co., Kyburz on Hwy. 50, *Koch 2146* (MICH). Madera Co., middle fork of San Joaquin R., *Koch & Koch 2198a* (MICH). Humboldt Co., near Groans hole, 41°-5'N, 123-29'W, *Norris 47832* (WTU). *Colorado:* Boulder Co., Rocky Mtn. Nat. P., N shore of Sand Beach Lake, *Hermann 27936* (COLO). 2 1/2 mi. WNW of Allenspark, *Hermann 25502* (COLO). 8 mi. NW of Eldora, *Hermann 24502* (COLO). Gilpin Co., 5 km. E of Corona Pass, *Shaw 2619* (ALTA). Park Co., North of Jefferson, *Weber, Porsild & Holmen*, 1960 (COLO). *Idaho:* Shoshone Co., 9 mi. NE of

Wallace, *Hermann 22560* (WTU). *Montana:* Lincoln Co., Cabinet Mountains, Leigh Creek, 6000 ft., *Flowers 6671* (COLO). Flathead Co., Lake Macdonald Trail, Glacier Nat. P., *Ireland 9953* (CANM). *Oregon:* Clackamas Co., Mt. Hood Area, above Timberline Lodge, *Shaw 2515* (ALTA). Mount Hood Meadows Ski area, *Shaw 2539* (ALTA). Next to Salhalie Falls, *Shaw 2519* (ALTA). Union Co., 20 mi. SE of Union, *Hermann 18873* (COLO). *Washington:* Snohomish Co: Mount Baker Nat. For., 3.5 mi. SE of Silverton, *Hermann 18520* (CANM). 0.25 mi. N of Barlow Pass, *Shaw 2332*. 4.9 km. N of Silverton, *Shaw 2345* (ALTA). East of Big Four, *Lawton 2432* (WTU). Pierce Co., S slope of Mt. Rainier, 5700 ft., *Hermann 18562* (CANM). Paradise Point, Mt. Rainier, *Shaw 2396* (ALTA). NW of Sunrise Point on Mt. Rainier, *Shaw 2454* (ALTA). Mount Rainier, *Andrews 9* (BH). Kitittas Co., 32 mi. NW of Cle Elum, 3000 ft., *Hermann 22699* (CANM). Mount Baker Area, *Shaw 2295* (ALTA). King Co., NW of Stevens Pass, *Lawton 4898* (WTU). *Wyoming:* Teton Co., Bradley Lake Trail, 7000 ft., *Shaw 2692* (ALTA). Signal Mountain, Summit road, 7200 ft., *Shaw 2704* (ALTA).

Pohlia camptotrachela can be characterized by 1) its spreading to erect-spreading, dull-green leaves which typically lack any hint of a sheen, wet or dry, and 2) its clusters of yellow to brown, globose, axillary propagula having 1-3-(5) poorly formed, peglike leaf primordia.

The propagula of *P. camptotrachela* are notably uniform in both color and shape, in contrast to those of such other species of the propaguliferous complex as *P. annotina*. The propagula arise in dense, axillary clusters, and are yellow-green to green when very young. Later in the growing season, the propagula are often uniformly translucent-yellow, although they sometimes become brown with age (although still translucent). They are consistently globose to shortly oblong (fig. 58), and the cells of the propagulum body are always roughly isodiametric. The apical leaf primordia arise as short, peglike outgrowths, and rarely elongate or become very conspicuous, often being incurved over the propagulum apex (fig. 58: 6, 8). When examining stems of *P. camptotrachela* under a dissecting microscope, the propagula appear to lack primordia altogether, although they are consistently present. They do not continue development after their initiation, usually remaining as unicellular outgrowths, never becoming conspicuous and laminal (cf. *P. annotina*, fig. 54). Lewis and Smith (1978), illustrated old, large, more bulbiform propagula of *P. camptotrachela*, which they said are occasionally encountered in the lower leaf axils of plants in the British Isles. I have not found such forms in North America, where the propagula are invariably small and densely clustered. For some reason, the propagula of North American plants do not grow to this same advanced stage of development, although otherwise the species is clearly the same on both continents. A similar situation has been noted with respect to the propagula of *P. annotina* (see pp.

Although the leaves of *P. camptotrachela* are almost invariably dull, a few specimens have been examined which had a distinct sheen to their leaves. However, in all other respects, including the propagula, the specimens agree closely with *P. camptotrachela,* and this is presumably an uncommon environmental modification.

Pohlia camptotrachela is very similar to, and probably most closely related to *P. annotina*. Both species have dull leaves, and have the perigonial bracts abruptly long acuminate from the ovate base, giving the perigonial plants an almost identical aspect (fig. 53: 15, 16; 57: 17, 18). Although similar in most morphological features, the two can usually be readily distinguished on the basis of propagulum morphology. The propagula of *P. annotina* are quite variable in color, but are rarely translucent-yellow as are those of *P. camptotrachela*. Those of *P. camptotrachela* are smaller (mostly ca. 120 um long), consistently globose or only slightly elongate, and are more or less abruptly narrowed to the stalk. In contrast, those of *P. annotina* are larger (mostly >175-200 um), extremely variable in shape, ranging from shortly obconic to elongate and narrowly sublinear or sometimes oblong and bulbiform, and are gradually narrowed to a shorter, less conspicuous stalk. Furthermore, the leaf primordia of *P. camptotrachela* propagula are short, peglike, and often incurved, while those of *P. annotina* are more elongate and fingerlike, erect, and often become more or less laminal on old propagula (see under *P. annotina*). The two are quantitatively compared in figure 59. Note that *P. annotina* is much more variable in all characters compared. Sometimes specimens are encountered in which propagula seem to be absent, and although a few can usually be found loose in the herbarium packet, when this is not the case, it is difficult or impossible to distinguish *P. camptotrachela* from *P. annotina*.

Pohlia camptotrachela, *P. annotina*, and the European *P. muyldermansii* seem to form a "subcomplex" within the propaguliferous Pohlias. They are all slender, dull plants, and I am unable to confidently distinguish them in the absence of propagula. The other species of the North American propaguliferous Pohlias are each usually distinguishable in the absence of propagula by a combination of features including size, pigmentation, leaf sheen and shape of the perigonial bracts, but in all these features, *P. camptotrachela*, *P. annotina* and *P. muyldermansii* seem to be identical (I have not seen male plants of the last species). This morphological similarity probably reflects phylogenetic affinity, but in spite of this close morphological similarity, propagula of the three species are distinct in nature, and remain distinct (in fact, they often become more distinct) in culture. Perhaps the species *P. camptotrachela*, *P. annotina* and *P. muyldermansii* differ somewhat in their precise biological meaning as compared to other species in the propaguliferous complex, which are more distinctive morphologically, but I feel that they warrant being treated at the specific level, at least for now. Although intergradation between *P. annotina* and *P. camptotrachela* is rare, a few specimens of the latter species from California have been examined which had the propagula somewhat more elongate, with the leaf primordia erect and more prominent than is typical for *P. camptotrachela*. It is almost an arbitrary decision to name such plants one species rather than the other, but I interpret them as aberrant forms of *P. camptotrachela*, and do not credit *P. annotina* to the state of California. *Pohlia camptotrachela* and *P. annotina* appear to be distinct also in Great Britain (Lewis and Smith 1978), so that excluding the possibility that one of them has arisen polyphyletically on the two continents, this is evidence that they have been distinct for some time (I think that recent, long distance dispersal is an unlikely explanation for their intercontinental distribution).

Pohlia camptotrachela has propagula which may appear similar to those of *P. andrewsii*, but these two species have geographic distributions which do not overlap. See under *P. andrewsii* for a morphological comparison.

9. *Pohlia proligera* (Lindb. *ex* Breidl.) Lindb. *ex* Arn., Bot. Not. 1894. 54. 1894.

Webera proligera Kindb., Forh. Vid. Sellsk. Christiana 1888(6): 30. 1888. *nom. nud.*

Webera proligera Lindb. *ex* Breidl., Mittheil. Naturwiss. Ver. Steirmark 28. 1891. Type: "Bei Schwanberg: Trager Wald 370 m, (!) Abhang der Koralpe 7-800 m.; Hitzelberg bei Mixnitz 5-700 m. (!); bei Wenigzell (!) Vorau (!) und Bruck a.d. Lafnitz. 6-900 m. (!); Hilmberg bei Friedberg (!) und Glashuttengraben am Wechsel 800 bis 900 m.; bei Rettenegg 870 m. (!); bei Krieglach (!) und im Veitschgraben 7-800 m.; bei Leoben; Bürgerwald und Schladnitzgraben 7-900 m. (!), Hochalpe 1640 m. (!); bei Judenburg: Murwald 700 m. (!), Feeberggraben 8-900 m. (Jur., B.); Wenzelalmkogel 1900 m. (!); am Fusse des Kreischberges bei Stadl 900 m. fr. (!); Turracher Hochalpe 17-1900 m. (!). ..., am Krahberg - und Steinkarzinken bei Schladming bis gegen 2000 m. (!); mit fr.: Schupfenberg bei Öblarn 12-1400 m. (Lectotype: GZU-Breidler !), Kraggau-Eben 1200 m., (!, isosyntype: H-SOL!), am Rainweg bei Schladming 800 m. (!). In der kalk- und Grauwackenzone, in Tragöss: an der Hieselegger Strasse 1000 m. fr. (!, Isosyntype: H-SOL !); auf der Neuwaldalm 14-1500 m. fr. (!)" (unless noted,all specimens are in

GZU-Breidler).

Webera annotina var. *proligera* (Lindb. *ex* Breidl.) Bryhn, Nyt. Mag. Naturv. 32(3). 124. 1892.

Webera annotina ssp. *proligera* (Lindb. *ex* Breidl.) Amann, Rev. Bryol. 20: 43. 1893.

Bryum proligerum (Lindb. *ex* Breidl.) Kindb., Eur. N. Am. Bryin. 2: 384. 1897.

Plants medium-size to robust, forming small, scattered populations or occasional extensive turfs, glossy when dry; stems 3-15-(25) mm. high, green above, green or sometimes red to red-black at the base especially when dry, simple or once innovating at the base when sterile, simple or occasionally once innovating below the perigonia when fertile; leaves erect-spreading to spreading and often somewhat flexuose but rarely twisted when dry, spreading to erect-spreading when moist, 0.7-1.2-(1.3) mm. long, 0.3-0.4-(0.5) mm. wide, ovate-lanceolate to narrowly lanceolate, acute, shortly decurrent by 1-3 rows of linear-rectangular cells, sometimes not at all decurrent; margins plane, toothed in the upper 1/2-1/3, entire or sometimes subentire in the lower 1/2; costa ending 2-4 cells below the apex, green in young leaves, green to red, red-brown or rarely black in older leaves; upper cells linear-rhombic to linear-rectangular, usually vermicular, thin-walled, (50)-65-90-(110) um long, (6)-7-9-(11) um wide, often with this complete range of dimensions present on a single leaf, somewhat longer and narrower in a poorly defined, single row along the margin, rectangular near the base, 3-6:1; asexual propagula abundant as a dense, almost felty layer in the upper leaf axils of sterile shoots, rarely scarce on old stems, scarce or absent when fertile, arising in clusters in each leaf axil, rather uniform in shape, oblong-linear to linear-vermicular, gradually narrowed to a uni- or biseriate stalk, mostly 150-300-(450) um long, but rarely only shorter, broader propagula present on old shoots, green when young, yellow to gold, orange or sometimes red when older, translucent, with 1-2 peglike leaf primordia at the apex, often (when single) bent at an angle to the propagulum body, the leaf primordia arising as unicellular, fingerlike outgrowths, rarely becoming 3 cells wide at the base; perigonia bulbiform, terminal on unbranched stems or the stems once innovating just below the perigonia; perigonial bracts abruptly acute to ± gradually acuminate from an ovate, concave, ± red-brown base; margins sharply toothed near the apex, sometimes to just above the shoulders; costa filling the narrow acumen; perichaetia terminal, inconspicuous; perichaetial bracts to ca. 2.6 mm. long, narrowly- to broadly lanceolate, often red at the base; costa strong, ending in the apex; median cells on average, somewhat longer than those of the vegetative leaves, to 125 um long, thin-walled; margins

± recurved from above the base to just below the apex, toothed in the upper 1/3. Dioicous; sporophytes infrequent; seta 2.0-3.0 cm. long, orange to orange-red; capsules positioned 90°-150° from the vertical, 1.5-2.5 mm. long, short- to ± elongate-pyriform, with a well developed neck which is ± shrunken when dry; orange to orange-brown when mature; exothecial cells longitudinally elongate and ± rectangular to irregularly isodiametric, mostly 25-55 um long, 13-23 um wide, with strongly sinuose walls, especially when dry, less so when moist, ± abruptly smaller, less sinuose and sometimes thicker-walled at the mouth, less sinuose in the neck, gradually elongate-rectangular just above the seta; stomata numerous in the neck, phaneropore, (32)-35-40-(46) um long; annuli well developed, of 2-(3) rows of cells, remaining attached to the urn or the operculum, sometimes separating irregularly or rarely ± revolvable; opercula convex to conic, apiculate; exostome teeth 16, yellow to yellow-brown above, sometimes darker below, lanceolate, narrowly acute, coarsely papillose in the upper 1/3, more finely papillose below; endostome segments 16, hyaline, keeled and broadly perforate; cilia (0)-1-3 between the segments, long, ± nodulose, rarely short; spores baculate, (15)-16-19-(23) um.; chromosome number N=11 (Ramsay 1969 - voucher not seen).

Nomenclature: *Pohlia proligera* was first distinguished conceptually by S.O. Lindberg as *Lamprophyllum (Pohlia) annotinum* var. *micans (in scheda !)*. Although several specimens dating from as early as 1861 (Stockholm in Solna-jkogen, 26 Sept. 1861, leg. S.O.L. !) bear this varietal epithet, the name was not published, to my knowledge. In the 1880's, J. Breidler began to send Lindberg specimens labelled *Webera annotina* from Austria in connection with Breidler's upcoming moss flora. While some such specimens were actually *P. annotina* (and were so named by Lindberg), others belonged to the taxon subsequently distinguished by Lindberg as *P. proligera*. By 1887, Lindberg (with his son Harold) had collected *P. proligera* in Norway (Tronfjeldt, Osterdalen!) and labelled the specimens *P. proligera* n.sp. *(in scheda)*. The name *Webera proligera* first appeared in print in 1888 (as a *nomen nudum*) in Kindberg's *Enumeratio Bryinearum Dovrensium*. In 1891, Breidler (1891) provided a description for the species, (as *Webera*), and acknowledged Lindberg (in litt.) for recognizing the plant as new, and for suggesting the epithet. The author citation for this species in *Webera* is then *W. proligera* Lindb. *ex* Breidler, and its validation dates from Breidler's publication, as was noted by Isoviita (in litt.), and Lewis and Smith (1978). Breidler cited a large number of syntypes in his protologue, and these are mostly well preserved in his herbarium in GRAZ (!).

Also on several herbarium sheets is written a note saying "*Webera proligera* Lindb. = *W. annotina* var. *micans* Lindb. ? *olim*." Shortly after Breidler's publication appeared, Bryhn (1892) and Amann (1893) reduced *W. proligera* to a variety and subspecies respectively, under *W. annotina*. Arnell (1894) made the combination *Pohlia proligera* in 1894 giving Lindberg (in litt.) credit for the combination, such that the correct citation should be *P. proligera* (Lindb. *ex* Breidl.) Lindb. *ex* Arn.

Distribution: (fig. 60). Numerous specimens of *P. proligera* have been examined from the northern and mountainous regions of North America. In Alaska, *P. proligera* has been collected from Pt. Barrow to the southern coast. In the Rocky Mountains it is confirmed from the Brooks Range south to Colorado, but no specimens have been seen from Arizona, New Mexico or Mexico. *Pohlia proligera* is likewise distributed widely in the coastal mountains from southern Alaska south to California, and no doubt additional collecting in the Sierra Nevada-Cascade Ranges will fill in the gaps of its known distribution in California and Oregon. Collections have been examined from scattered localities in the Northwest Territories and Greenland, and the species seems to be not uncommon in the southern maritime provinces. A few collections have been made in New York and New England, and in the midwest *P. proligera* is known from Michigan, Wisconsin and Illinois. Non North American specimens have been examined from Austria, Czechoslovakia, England, Federal Republic of Germany, Greenland, Italy, Norway, Poland, Sweden and the Kola Peninsula, U.S.S.R.

Selected Specimens Examined: Exsiccati. Several exsiccati sets which contain more than one species in mixture or which differ from one herbarium to another have greatly confounded the taxonomic uncertainty already surrounding the propaguliferous Pohlias. With the hope of clearing up a few of the confusing problems surrounding some such cases, I include here a brief discussion of several, critical exsiccati specimens.

Holzinger, Musci Acrocarpi Boreali-Americani et Europaei 663 as *P. proligera*.* This number of Holzinger's exsiccati was distributed in 1929 (Sayre 1971). In the Bryologist (32: 61) of 1929, Holzinger wrote that No. 663 is not *P. proligera* and promised a further note. Shortly thereafter, following Holzinger's death in 1929, Andrews (1929) provided the further note (since he had determined Holzinger's original specimen for the exsiccati). Andrews (1929) wrote that he had reexamined a specimen of that number and confirmed that it was indeed *P. proligera*, but offered no explanation for Holzinger's original note. In 1930, Andrew's further discussed the problem and said that he had just received a letter which Loeske had written to Holzinger dated 20 May 1929 (Mrs. Holzinger had sent the letter to E.B. Bartram after her husband's death, and Bartram sent it to Andrews). In that letter, Loeske told Holzinger that his (Loeske's) specimen of no. 663 was *P. drummondii* (as *P. commutata*), and included no *P. proligera*. That was the reason for Holzinger's (1929) first communication. Andrew's, however, said all the duplicates he had seen were *P. proligera*. Loeske (1930) then published a further note saying that his specimen was definitely *P. commutata* (with propagula) and suggested that "the material must have been mixed by the collector or, better said, by nature." Of the specimens which I have examined (DUKE, NY, MO, MICH, WIS, CANM, BH, MINN, WTU, COLO), all are *P. proligera* except for that at the last cited herbarium (COLO), which is *P. drummondii*. F. A. MacFadden, who collected the exsiccati for Holzinger, must have accidently picked up just a bit of *P. drummondii* in mixture with the *P. proligera*. Concerning another of Holzinger's collections (no. 114 of the same exsiccati, as *P. proligera*), Loeske said that Holzinger had sent a specimen to Kindberg, who "pronounced it a new species and asked Holzinger to describe it." Fortunately, Holzinger declined, and Loeske added that "Holzinger's no. 114 agrees with authentic European specimens of *P. proligera* like one egg for another." I quite agree with Loeske.

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* Reference to this literature was provided by H. Crum on the exsiccati specimen of this number in CANM.

Allen, Mosses of the Cascade Mtns. no. 54 as *P. proligera*. Lawton (1971) noted that this exsiccati number includes both *P. proligera* and *P. annotina* in most herbaria. I can offer the following observations. In H, No. 54 is completely *P. proligera*. In UBC, NY, MO, MICH, and COLO, specimens are mostly *P. annotina,* but include a few shoots of *P. proligera*. The specimen in US is mostly *P. proligera* but includes a few shoots of *P. annotina*.

Macoun, Canadian Musci 162 as *W. annotina*. This exsiccati number is by far the most heterogeneous and confused of any I have encountered. Sayre (1971: 129) discussed some of the criticisms which have been leveled against Macoun and Kindberg's bryological activities saying particularly that their herbarium practice seems not "to have been sufficiently scrupulous". On the basis of Canadian Musci no. 162, I would say that Dr. Sayre was being kind, to say the least. The following are those elements I have so far encountered under no. 162: WIS - *P. annotina;* MIN - *P. filum;* H - *P. nutans;* MO - *P. proligera;* US - two specimens, one specimen is *P. wahlenbergii,* and the other is *P. proligera*.

North America: Allen, Mosses of the Cascade Mtns. 54 as *P. proligera* (H (completely), COLO, MICH, MO, UBC, US (in part); Bauer, Musci Europ. et Amer. Exs. 1736 as *P. proligera*

(COLO, MINN, WTU); Holzinger, Musci Acro. Bor.-Am. 114 as *W. proligera* (COLO, DUKE, H, MICH, MIN, MO, US, MINN, NY, US, WTU); 663 as *P. proligera* (BH, DUKE, MICH, MIN, NY, WTU); Macoun, Can. Musci 162 as *W. annotina* (NY, MO, US); 463 as *W. proligera* (CANM - in part); Macoun, Flora Can. 193 as *B. annotinum* (CANM); 1117 as *B. annotinum* (CAS); Ren. & Card., Musci Amer. Sept. Exs. 379 as *W. proligera* (MIN). Europe: Bauer, Musci Eur. Exs. 1099a as *P. proligera* (WTU, F, COLO); Bauer, Musci Eur. et Amer. Exs. 1776a as *P. proligera* (MO, WTU); 1776b as *P. proligera* (MO, WTU); 2026 as *P. proligera* (WTU, CANM); Brotherus, Bryoth. Fenn. 46 as *P. proligera* (BH, F); Cryptogamae Exs. 3771 as *W. annotina* (US, COLO, MO - all in part); Hartman, Bryaceae Scand. Exs. 14 as *W. annotina* (BH, COLO); Husnot, Musci Galliae 873 as *P. proligera* (F, BH); Kopsch, Bryoth. Saxonica 241 as *P. proligera* (U); Lisowsky, Bryoth. Polonica 731 as *P. proligera* (CANM, US); 509 as *P. proligera* (U); Migula, Crypt. Germ, Aust. & Helv. Exs. 250 as *W. proligera* (BH, MICH, MO, UBC, US); Pilous, Musci Czech. Exs. 519 as *P. proligera* (F); 1135 as *P. proligera* (F, US); 1048 as *P. proligera* (BH). Canada. *Alberta:* Grand Cache area, Beaver Dam Cr., *Koponen 23784* (H). Ft. McMurray area, tarsand bank along rd. leading to Horse River, *Douglas & Peterson 5145* (ALTA). Willmore Wilderness area, 8.3 mi. (1 mi. = 1.6 km.) W of gate into park at Rock Lake, *Vitt 13988* (ALTA). Jasper National Park, Maligne Lake area, Bald Mtn. Trail, *Shaw 2836* (ALTA). Signal Mtn. Trail, *Shaw 2990* (ALTA). Onoway area, 3 mi. E of Onoway along the Sturgeon River, *Shaw 1424* (ALTA). Trail from Waterton Lakes to Alderson Lake, *Crum & Schofield 5877* (UBC). Mountain Park area, 22.2 mi. S of Cadomin, *Vitt 10979* (ALTA). *British Columbia:* Sanden, *MacFadden 754* (BH). Mi. 84 (1 mi. = 1.6 km.), Haines Hwy., *Crum & Schofield 9157* (CANM). Glacier Nat. P., along Avalanche Crest Trail, *Shaw 2153* (ALTA). Revelstoke area, 10 mi. S of Revelstoke at Blanket Creek cmgd., *Shaw 2193* (ALTA). Manning Prov. P., Shadow Falls Trail, *Shaw 2267* (ALTA). Nelson area, Kokanee Cr. at Redfish cmgd., *Shaw 2758* (ALTA). *Labrador:* Churchhill Falls area, 53°36'N, 64°19'W, *Brassard 7203* (NFLD). Kaipokok Bay, vicinity of Three Rapids Camp, *Brassard 11677* (NFLD). *Ontario:* Thunder Bay district, S of Upsala, *Cain,* 1944 (BH). Algoma district, *Sharp,* 1960 (TENN). *New Brunswick:* Restigouche Co., 1.5 mi. S of St. Jean-Baptiste-de-Restigouche, *Ireland 14524* (CANM). Westmorland Co., 12 mi. SW of Salisbury, *Ireland 13543* (CANM). *Newfoundland:* Ryan's Brook, 47°52'N, 59°14'W, *Belland 354* (NFLD). Biscay Bay, Ferryland, *Tuomikoski 358* (H). Ha-Ha Bay, *Tuomikoski 3698* (H). Rattling Brook, *Brassard 11039* (NFLD). *Northwest Territories:* Mackenzie Mtns., Liard Range, NW of Sawmill Mtn., *Vitt 20588* (ALTA). Ellesmere Isl., 5 km. S of Tanquary Camp, *Brassard 3318a* (NFLD). Island of Silumiut, Hudson Bay, *McCartney AB 1/2*

(MICH). Mouth of Copper River, *Steere 10772* (NY). Great Bear Lake, NE tip of Hornby Bay, *Steere 10506* (NY). *Quebec:* Nouveau-Quebec: environs de Puvirnitug, *Bournerias 701705* (H). Iles-de-la-Madeleine, Ile d'Entree, *Sloover*, 1968 (NFLD). Gaspe Nord, *Crum & Williams 10654* (MICH). Gaspe, Mt. Sainte Anne, *Fabius 5210* (BH). *Yukon:* Mile 1022, Alaska Hwy., Little Bear Cr., *Crum & Schofield 8960* (CANM). Hunter Creek, *Macoun 179* (CANM). Hess Mtns, Rogue Range, Emerald Lake, *Vitt 23555* (ALTA). Gribbles Gulch at mile 120 on Haines Hwy., *Vitt 12753* (ALTA). Dezadeash Lake, *Vitt 12716* (ALTA). U.S.A. *Alaska:* Pt. Barrow & vicinity, *Steere 16357* (NY). Meade River Camp, *Steere 15794* (NY). Bettles, Koyukuk River, *Sherrard 25-6* (CANM). Mt. Mckinley region, Katishna, *Sherrard B 44* (CANM). Thum Bay, Knight Island, *Everdam 740* (BH). Harrison Bay Quadrangle, National Petroleum Preserve, *Murray 77-874* (ALA). Brooks Range, Anaktuvik Pass, *Steere, Inoue & Iwatsuki 678* (NY). *California:* Siskiyou Co., Mt. Shasta, *Koch 15657C* (UC). Lassen Co., N end of Butte Lake, *Showers 3617a* (MICH). *Colorado:* Pitkin Co., ca. 5 mi. E of Aspen on Hwy. 82, *Shaw 2548* (ALTA). Gilpin Co., 20 km. W of Rollinsville on Corona Pass Rd., *Shaw 2603* (ALTA). Boulder Co., ca. 10 mi. E of Netherland on Hwy. 119, *Shaw 2665* (ALTA). Grand Co., 8 1/2 mi. N of Grand Lake, *Hermann 26605* (COLO). *Idaho:* Gibbonsville area, just S of Lost Trail Pass on Hwy. 93, *Shaw 2718* (ALTA). Adams Co., 4 mi. E of New Meadows, *Hermann 20271 1/2* (US). *Illinois:* Lasalle Co., Starved Rock St. P., *Redfearn 29144* (SMS). *Michigan:* Alger Co., Train Bay, *Sharp,* 1955 (MICH). Luce Co., Upper Tahquamenon Falls, *Crum,* 1966 (MICH). Keweenaw Co., Near Copper Harbor, *Steere,* 1935 (MICH). Marquette Co., shore of Lake Superior, *Hermann 28528* (DUKE). *Minnesota:* Lamoille Cave, *Holzinger,* 1894 (MIN). Cook Co., just N of Grand Marais on Lake Superior, *Bowers 716* (MIN). *Montana:* Lincoln Co., Cabinet Mtns., *Flowers 6671* (COLO). Teton Co., Phelps Lake Trail Canyon, *Osweld 1384* (COLO). *New York:* Essex Co., upper slopes of Mt. Whiteface, *Smith 49707* (NYS). *Vermont:* Newfane, Baker Brook Gorge, *Andrews,* 1936 (BH). *Washington:* Snohomish Co.,Mt. Loop Hwy., 0.25 mi. N of Barlow Pass, *Shaw 2337* (ALTA). Pierce Co., Mt. Rainier area, *Shaw 2444* (ALTA). Skamania Co., Mt. St. Helens area, *Shaw 2501* (ALTA). *Wisconsin:* Grant Co., near Patch Grove, *Cheney 12459* (WIS). Barren Co., along Vermilion River, *Cheney 5114* (WIS). Richland Co., Rockbridge Park, *Nee 13182* (SMS). *Wyoming:* Teton Co., Teton Nat. P., Bradley Lake Trail, *Shaw 2702* (ALTA). Yellowstone Nat. P., Crescent Hill, *Conard,* 1953 (CANM). Albany Co., Centennial Valley, *Nelson 1723* (WTU).

Pohlia proligera is almost invariably an easily distinguished species characterized by its 1) glossy leaves and 2) linear-vermicular, clustered, axillary propagula with one or two peglike leaf primordia. The propagula of *P. proligera* are notably uniform in shape, being consistently narrow and linear-vermicular, not becoming large or bulbiform on old stems as do the propagula of some species such as *P. andalusica* or *P. annotina*. Several populations in Alberta which have been under observation from September 1977 until October 1979 have failed to produce large, bulbiform propagula at any season of the year, and samples grown in a greenhouse have likewise failed to exhibit any substantial degree of developmental variation in morphology. In late spring (early June in Alberta), young shoots of *P. proligera* have a dense, feltlike, seemingly continuous layer of green, vermicular propagula among the upper leaves. These propagula obtain their typical shape (e.g. fig. 62: 9) within a week or two of their initiation on young shoots, and usually do not develop further during the course of the growing season. In this respect, propagula of *P. proligera* can be described as determinate in their growth. The same populations observed in July or August have very similar propagula, although they may have become golden or red in color and slightly fewer as some have become disattached and have fallen to the ground. Observations in September, October, or up until the first snowfall have, in every case, confirmed the morphological stability of propagula during the course of a complete growing season. Shortly after the snow has melted in the following spring, it is possible to continue observations on the same populations before any growth has begun during that current season. Old stems of the previous year then have few propagula, and these are almost always distinctly red-translucent at this stage. Even these propagula, however, have failed to continue growth, and fall within the morphological range illustrated in figure 62. Sometimes the relatively few propagula present at this time of year are predominantly short and oblong-linear (e.g. fig. 62: 3), rather than narrowly, linear-vermicular as they are when in dense, fresh clusters on newly formed shoots (e.g. fig. 62: 16-22). These field observations are in agreement with ongoing culture studies, and also with extensive herbarium studies in which the propagula of *P. proligera* have been found to be very uniform in morphology. However, I should add that this nonvariability could be a function of shoot growth phenology, and that populations growing at lower latitudes (if they be found) may have different phenologies and developmental pathways and, consequently, different patterns of morphological variability.

Of the species with clustered propagula, *P. proligera*, *P. bulbifera*, *P. andalusica*, *P. tundrae* and *P. andrewsii* have leaves with a distinct gloss when dry. The bulbiform propagula of *P. bulbifera* and *P. andalusica* easily distinguish these two species from *P. proligera*, and they have rarely been confused in the past. For the characteristics distinguishing *P. tundrae* from *P. proligera*, see under the former species, and to distinguish *P. proligera* from *P. andrewsii*, see under the latter species.

Pohlia annotina and *P. camptotrachela* are morphologically similar species with clustered propagula and nonglossy leaves (see also discussion under *P. camptotrachela*). With very rare exceptions, these species are readily distinguished from *P. proligera* by their smaller size and nonglossy leaves, as well as by the morphology of their propagula. The long, slender propagula of *P. muyldermansii* (not known from North America) may appear superficially similar to those of *P. proligera*, but are considerably longer (mostly > 500 um. long), and have 1-3 very short peglike leaf primordia which are hardly more than 1/10 the length of the propagulum. The small, more or less sphaeroidal propagula of *P. camptotrachela* are unlike any form produced by *P. proligera*, and are smaller, rounder, and have less conspicuous leaf primordia than even atypically short propagula of *P. proligera* (e.g. fig. 62: 1-7).

Pohlia proligera has most frequently been confused with forms of *P. annotina* in which the clustered propagula are unusually long (e.g. 350 um.) and narrow. See under *P. annotina* for a discussion comparing these two species.

Doubtful and Excluded Species

Webera polymorphoides Kindb. *in* Macoun & Kindb., Cat. Canad. Pl. 6: 113. 1892. This species was described by Kindberg (1892), and was later placed in synonymy of *Pohlia drummondii* by Andrews (1935). The type, however, is paroicous and the leaves are concave and cucullate, and have large, lax leaf cells (greater than 15 um. wide). It is consequently considered a synonym of *P. obtusifolia* (Brid.) L. Koch, rather than *P. drummondii* (Lectotype: "Canada, Selkirk Mtns., boggy soil, 7000 ft. 1 Aug. 1890. Macoun. S-Kindb. !).

Webera debatii Card. & Ther., *Bryum naviculare* Card., *Webera annotina* var. *curvicollis* Ren. & Card. I have been unable to obtain type material for these taxa (PC - presumably), and consequently they must be included as doubtful. Cardot (1900) indicated that *B. naviculare* Card. is synonymous with *Webera carinata (= P. filum)*.

Bryum geniculatum Brid., Musc. Rec. 2: 53. 1803. Bridel included *B. geniculatum* in his"*Brya incerta non genuina*", referring to Villars' - 1786-flora. No specimen so-named exists in the Bridel herbarium (Schultze-Motel in litt.).

Webera rubella Rhilibert, *W. subannulata* Philibert. Type material for these species either does not exist in the Philibert herbarium, or is not available for loan.

PHYTOGEOGRAPHY AND CONCLUSIONS

Of the nine propaguliferous Pohlias of the section *Pohliella* which occur in North America, only one species, *P. tundrae*, appears to be restricted to this continent. The remaining eight species are presently confirmed as occurring in Europe, and *P. drummondii*, *P. filum*, *P. bulbifera*, *P. annotina* and *P. proligera* are also reported from northern Asia (Nyholm 1958). This complex of species appears largely restricted to the northern latitudes of the northern hemisphere, and only *P. bulbifera* can be confirmed in the southern hemisphere (New Guinea) as a result of this study. In and around the tropics, this complex of propaguliferous species is mostly or completely replaced by members of the "*P. flexuosa* group" (see pp. 8,9) and species of the genus *Pseudopohlia*. Although specimens from Mexico and Central America have been examined which have propagula similar to those of *P. annotina*, these plants differ in other gametophytic and sporophytic features such that it is clear that the similarity in propagulum morphology is because of convergent evolution in this respect. The report by Griffin (1972) of *P. annotina* in Guatamala is based on such plants which have propagula not unlike those of *P. annotina*, but which have sporophytic characteristics unlike any member of the section *Pohliella* (Guatamala, Depto. De Jalapa, Dixon

014323 FLAS !).

Most bryologists agree that long distance dispersal is not as common in mosses as was once thought (e.g. Crum 1972, van Zanten 1976), and that the distribution of moss species is controlled by similar factors to those which control vascular plant distributions. If the transcontinental distribution of these *Pohlia* species is not the result of recent long distance dispersal, then their present distribution must indicate a considerable age for the taxa. North America and Europe have not been in physical contact since the early to mid Tertiary (Dietz and Holden 1970), so it is likely that the modern propaguliferous species date to at least that time period. That there are little or no morphological differences between North American and European populations of the same species indicates that evolution has occurred very slowly over the last 40-65 million years. This is in agreement with the opinions of other authors concerning the slow rate of bryophyte evolution (e.g. Crum 1966, 1972).

Based on similarities and differences in propagulum ontogeny, figure 63 shows a suggested phylogenetic arrangement of these propaguliferous *Pohlia* species. It can be seen that ecological data correlate with the presumed direction of structural evolution. Species which are characterized by morphologically primitive (plesiomorphous) features, tend to occur on substrates with relatively high levels of organic matter content, while those having a predominance of derived (apomorphous) character-states occur on substrates with a lesser amount of organic matter. Further, species with primitive character-states tend to occur on substrates of intermediate pH values, while those with derived character-states occur on soils of either high or low pH. Although *Pohlia filum* is considered primitive morphologically, this species appears specialized ecologically (fig. 63). Finally, morphologically primitive species tend to occur in alpine tundra, while derived species are more common in lowland to montane, man-made habitats.

On the basis of this correlation between ecology and morphology, it can be suggested that the ecologically primitive condition for these species is to occur in alpine tundra of high organic matter content and with the pH in the range 5.2-5.8. Evolution has occurred toward substrates with lower organic matter, and with either higher, or lower average pH values. Either the immediate ancestor of these species was an alpine plant, or very early in the diversification of the modern propaguliferous species, the primitive morphological types were restricted to tundra habitats. Recent authors have suggested that alpine plants began to evolve in the mid-Tertiary, and this is consistent with the minimum age suggested for these *Pohlia* species (Billings 1974, Mathews 1979).

In North America, some species of this complex are more restricted geographically than others. *Pohlia camptotrachela* is the most restricted species, and is known only from the western mountains, largely south of the maximum extent of glaciation (fig. 56). No collections of *P. camptotrachela* have been seen from north of Revelstoke, British Columbia, and it is clear that this species must have survived glaciation south of the ice sheet. That it has not migrated farther north, particularly along the Pacific Coast where the bedrock is siliceous, implies that *P. camptotrachela,* even with its abundant propagula and sporadic sexual reproduction, has only a limited ability to expand its geographic range rapidly. The distribution of *P. tundrae* (fig. 41) in the mountains of western United States is similar to that of *P. camptotrachela,* but *P. tundrae* occurs in Utah and Nevada where *P. camptotrachela* is absent. *Pohlia tundrae* is also disjunct in northernmost British Columbia, and in the southern part of Alaska. It is not common in these regions, however, and its occurrence may be the result of several instances of long distance dispersal from the southern portion of its range. Parts of the Queen Charlotte Islands and other areas along the southern and southeastern coasts of Alaska were apparently ice-free during at least parts of the Pleistocene (Karlstrom and Ball 1969, Schofield 1969), and it is also possible that populations of *P. tundrae* survived glaciation in these areas.

Pohlia drummondii and *P. andalusica* are known from scattered localities in the western mountains, and also occur in the northeastern portions of North America (fig. 32, 38). *Pohlia drummondii* has been collected more frequently than *P. andalusica*, and this seems to reflect their relative abundance in most areas. Neither species has been collected from a large portion of north-central North America, and probably the high pH of the soil in much of northern Alberta, Manitoba, Saskatchewan and the Northwest Territories is the cause of their absence or scarcity in these regions. Both species occupy a range that was largely glaciated during the Pleistocene. It is likely that they migrated southward during the Pleistocene, and have recolonized much of their previous area following retreat of the ice front. It is also possible that some populations survived in unglaciated refugia such as Beringia (Hulten 1937). *Pohlia filum* has a distribution similar to the previous two species (fig. 35), but is not known from the Rocky Mountains south of Alberta. In the Cascade range, *P. filum* extends only as far south as southern Oregon. Like *P. drummondii* and *P. andalusica*, *P. filum* probably survived glaciation south of the ice sheet, as well as in scattered refugia within the area of glaciation. *Pohlia bulbifera* likewise is known from scattered localities, mostly within the area of glaciation (fig. 45), and probably survived in widely disjunct localities. This species seems not to have expanded its range greatly from these separated stations during the Holocene. *Pohlia proligera* occupies the widest range, and has been most abundantly collected of any North American propaguliferous *Pohlia* (fig. 60). It is recorded from localities across boreal, sub- and low arctic North America, and extends southward in both the Cascade-Sierra Nevada Ranges and in the Rocky Mountains. It is likely that *P. proligera* survived glaciation both north and south of the maximum extent of glaciation.

Pohlia annotina has a bryogeographically interesting, bicentric distribution in North America (fig. 52). In eastern North America, *P. annotina* extends as far south as Arkansas, and extends no farther north than a few hundred kilometers north of the Pleistocene ice boundary. Eastern populations of *P. annotina* probably survived glaciation south of the ice sheet. In the western portion of its range, however, *P. annotina* is largely restricted to the area north of the maximum extent of glaciation. It is frequent along the coast of British Columbia and southern Alaska, and probably survived glaciation in coastal refugia which probably existed during the Pleistocene (Heusser 1960). Although the western and eastern populations of *P. annotina* are widely separated at present, and have probably been so since at least the last interglacial, there has been no significant morphological divergence between eastern and western populations.

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TABLE 1. Correct nomenclatural citations for the propaguliferous species in *Pohlia* with a partial list of synonymy.

SPECIES CITATION	IMPORTANT SYNONYMS
1. *Pohlia drummondii* (C. Müll.) Andr.	*Webera commutata* Schimper, 1876 *Webera catenulata* Schimper, 1876
2. *Pohlia filum* (Schimper) Mårt.	*Bryum ludwigii* var. *gracile* B.S.G., 1839 *Webera erecta* A. Roth *ex* Corr., 1899 *Webera rothii* Corr.*in* Limpr. & Limpr. f., 1902
3. *Pohlia andalusica* (Höhnel) Broth.	*Webera annotina* var. *glareola* Ruthe & Grebe, 1901 *Pohlia hercynica* Warnst., 1913 *Pohlia rothii* (Corr. *ex* Limpr.) Broth., *fide* Loeske 1905, Lewis & Smith 1978
4. *Pohlia tundrae* J. Shaw	*Pohlia annotina* var. *decipiens* Loeske *fide* Flowers 1973
5. *Pohlia bulbifera* (Warnst.) Warnst.	*Webera bulbifera* Warnst., 1896
6. *Pohlia andrewsii* J. Shaw	*Bryum annotinum* Hedw., *fide* Lindberg 1867

(Continued)

TABLE 1. (Continued)

SPECIES CITATION	IMPORTANT SYNONYMS
7. *Pohlia annotina* (Hedw.) Lindb.	*Pohlia grandiflora* H. Lindb., 1900 *Pohlia camptotrachela* (Ren. & Card.) Broth., *fide* Index Muscorum *Pohlia proligera* (Kindb. *ex* Breidl.) Lindb. *ex* Arn., *fide* Lewis & Smith 1978
8. *Pohlia camptotrachela* (Ren. & Card.) Broth.	*Webera camptotrachela* Ren. & Card., 1886
9. *Pohlia proligera* (Lindb. *ex* Breidl.) Lindb. *ex* Arn.	*Webera proligera* Lindb. *ex* Breidl.

TABLE 2. Summary of statistics relating to utilization of soils of varying pH realized niche = 100% of populations; central niche = 30% of populations; niche breadth = 1 standard deviation of the mean. Integers following species names indicate their order in the systematic section.

SPECIES	MEAN	REALIZED NICHE	CENTRAL NICHE	NICHE BREADTH (standard deviation)
P. drummondii (1)	5.70	4.58-8.15	5.47-5.78	0.60
P. filum (2)	5.83	4.99-8.09	5.52-5.85	0.62
P. andalusica (3)	5.77	5.12-6.86	5.51-5.89	0.58
P. tundrae (4)	5.61	4.79-6.69	5.42-5.79	0.46
P. annotina (7)	5.48	4.38-6.75	5.27-5.73	0.59
P. camptotrachela (8)	5.54	4.79-6.46	5.42-5.69	0.35
P. proligera (9)	5.93	4.30-7.58	5.74-6.17	0.58

TABLE 3. Summary of statistics relating to utilization of soils of varying % organic matter content, realized niche = 100% of populations; central niche = 30% of populations; niche breadth = 1 standard deviation of mean. Integers following species names indicate their order in the systematic section.

SPECIES	MEAN	REALIZED NICHE	CENTRAL NICHE	NICHE BREADTH (standard deviation)
P. drummondii (1)	2.35	0.95-3.15(-100)	2.25-2.70	0.61
P. filum (2)	1.23	0.60-2.40	1.10-1.32	0.31
P. andalusica (3)	2.27	1.85-2.85	2.00-2.50	0.38
P. tundrae (4)	2.37	1.30-3.35	2.30-2.65	0.46
P. annotina (7)	1.88	0.50-3.30	1.35-2.30	0.73
P. camptotrachela (8)	1.44	0.80-2.70	1.25-1.47	0.47
P. proligera (9)	2.08	0.70-3.10	1.90-2.40	0.61

TABLE 4. Significance of ecological differences by the Wilcoxon Signed-rank test.
*** 0.000-0.009; ** 0.0010-0.0099; * 0.0100-0.0490
1 - ph; 2 - organic matter (OM).

	P.campto-trachela	P.proligera	P.annotina	P.tundrae	P.filum
P. drummondii		*			
P. filum	*		*		
P. tundrae		**			
P. annotina		***			
P. proligera	***				

	P.camptotrachela	P.proligera	P.annotina	P.tundrae	P.filum
P. drummondii	***	*	**		***
P. filum		***	***	***	
P. tundrae	***	*	**		
P. annotina	***				
P. proligera	***				

TABLE 5. Statistically significant ecological differences between selected propaguliferous Pohlias. OM = substrate % organic matter; pH = substrate pH.

	P.camptotrachela	*P.proligera*	*P.annotina*	*P.tundrae*	*P.filum*
P. drummondii	OM	OM pH	OM		OM
P. filum	pH	OM	OM pH	OM	
P. tundrae	OM	OM pH	OM		
P. annotina	OM	pH			
P. proligera	OM pH				

9

TABLE 6. Herbaria from which propaguliferous Pohlias were examined. Asterisks after herbaria abbreviations indicate that only type specimens or a limited number of collections were examined.

ALA
ALTA
B*
BH
BM*
BP*
CANM
CAS
COLO
Crundwell - Priv. Herb.
DUKE
F
FH
G*
GOET*
GRAZ*
H
LAF
MAK*
MANCH*
MICH

MIN
MO
NFLD
NY
O*
PAC
S*
SMS
SMU
NYS
TENN
TRH*
U*
UAC
UBC
UC
US
WIS
WTU
Z*

FIGURE 1. Leaves and leaf cells

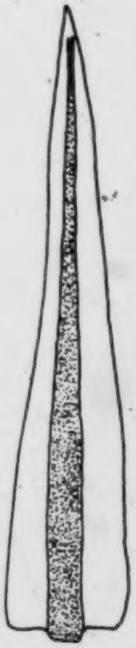
1-6 *Pohlia proligera* (Lindb. *ex* Breidl.) Lindb. *ex* Arn., differentiation of leaves on a female plant from stem apex (left) toward base (right) (x36)

7,8 *Pohlia drummondii* (C. Müll.) Andr., leaves from sterile plant (x36)

9 *Pohlia ludwigii* (Spreng. *ex* Schwaegr.) Broth., leaf from sterile plant (x36)

10 *Pohlia bulbifera* (Warnst.) Warnst., upper median leaf cells (x390)

11 *Pohlia tundrae* J. Shaw, basal cells (x390).



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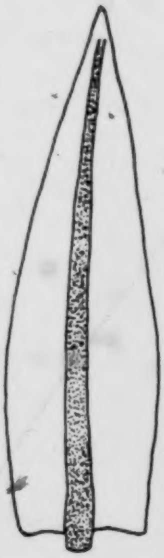

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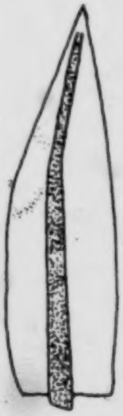

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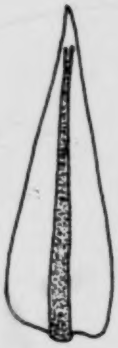

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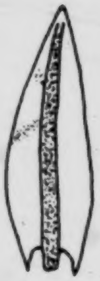

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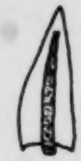

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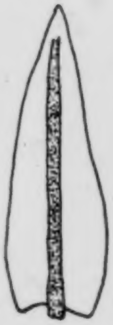

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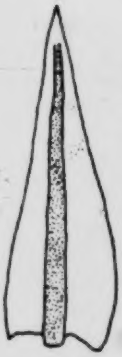

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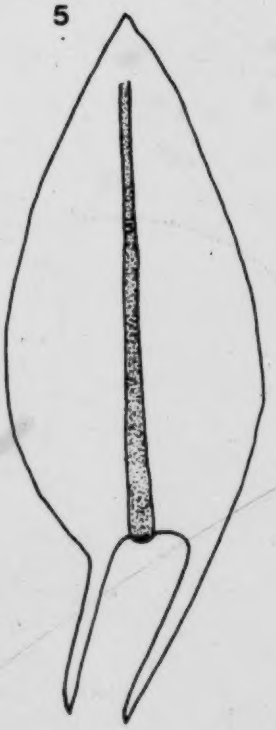

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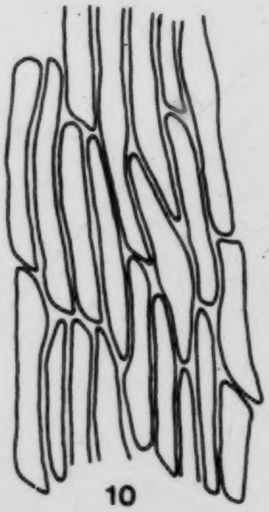

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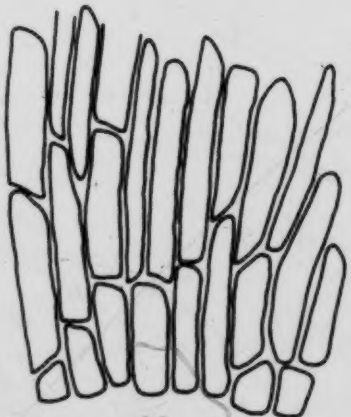

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FIGURE 2. Stems and leaves; transverse sections

1-3 *Pohlia andrewsii* J. Shaw, leaf sections from apex (1) to base (3) (x390)

4 *Pohlia annotina* (Hedw.) Lindb., perichaetial bract, transverse section (x390)

5,6 *Pohlia drummondii* (C. Müll.) Andr., stem transverse sections from near base (5) and apex (6) (x390).

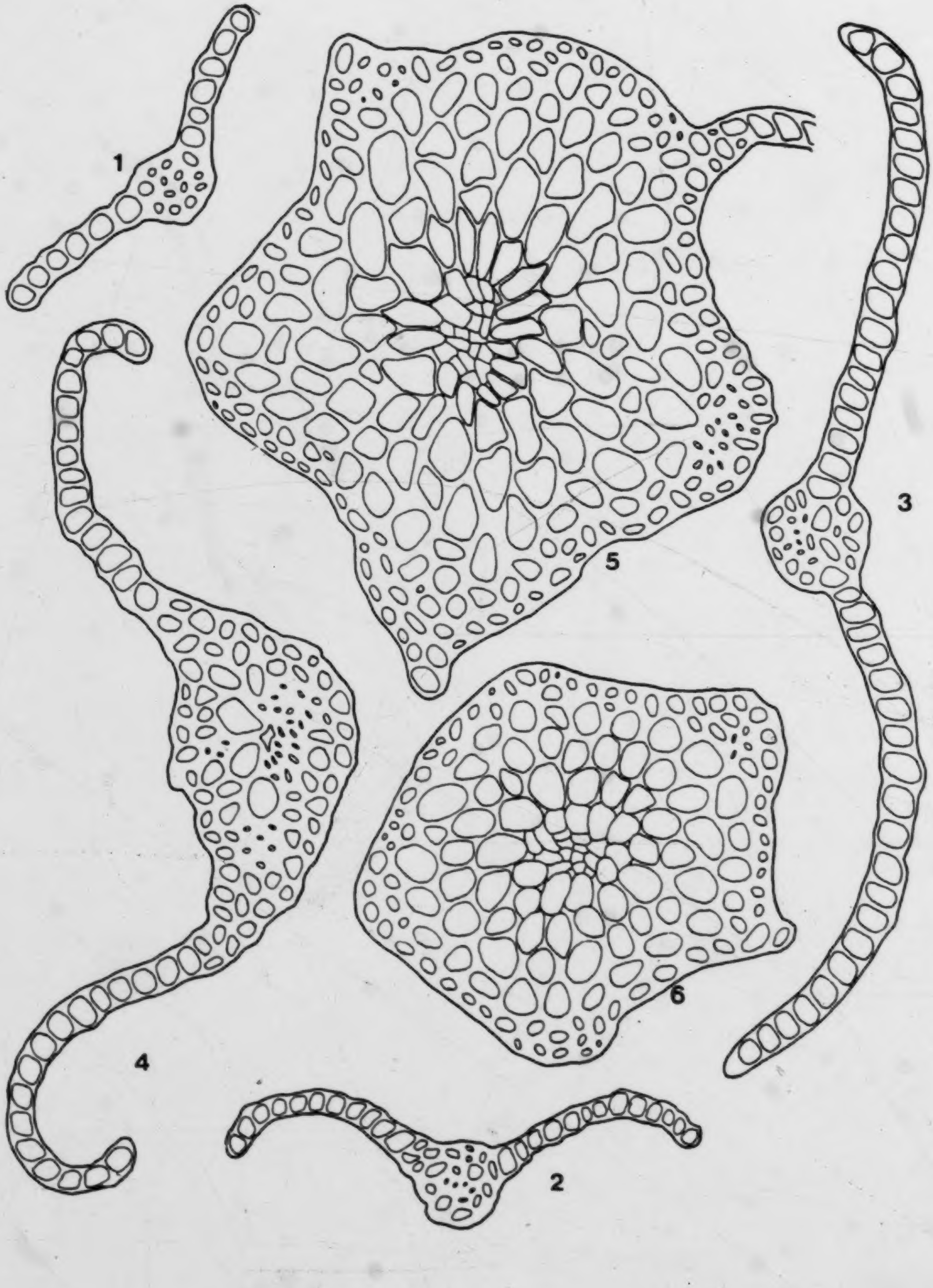
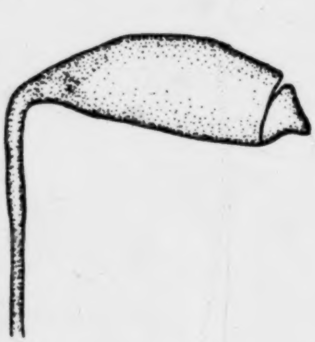


FIGURE 3. Perigonial bracts, setae in transverse section, capsule habit

1-6 *Pohlia bulbifera* (Warnst.) Warnst., differentiation of perigonial bracts from outside (1) to inside (6) (x36)

7,8 *Pohlia filum* (Schimper) Mårt., setae in transverse section showing size variation (x36)

9-11 *Pohlia drummondii* (C. Müll.) Andr., 3 capsules from one population showing variation in habit (x12).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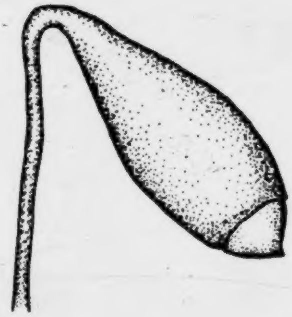
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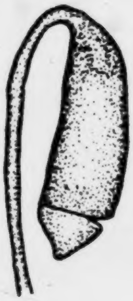
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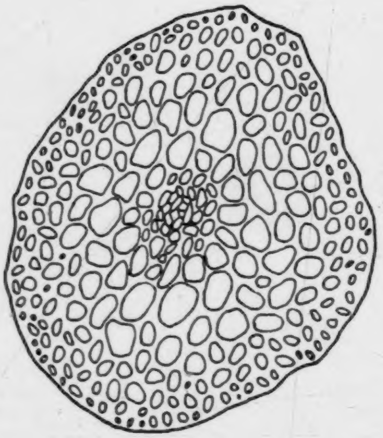
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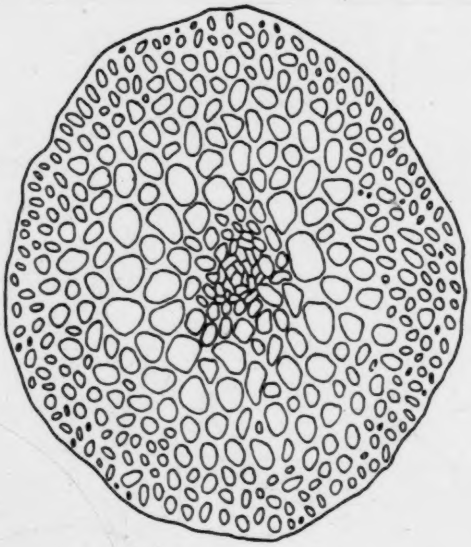
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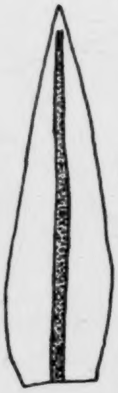
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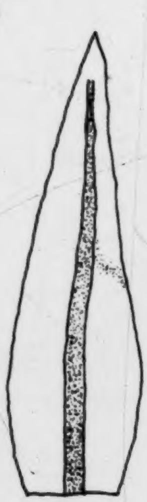
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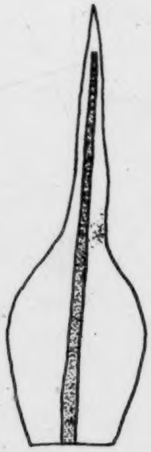
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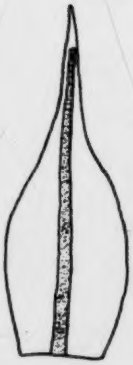
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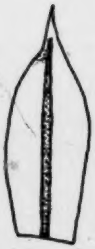
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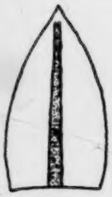
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FIGURE 4. Outer perigonial bracts (x36)
1,2 *Pohlia andalusica* (Höhnel) Broth.
3 *Pohlia bulbifera* (Warnst.) Warnst.
4 *Pohlia tundrae* J. Shaw
5,6 *Pohlia proligera* (Lindb. *ex* Breidl.) Lindb. *ex* Arn.
7 *Pohlia annotina* (Hedw.) Lindb.
8 *Pohlia camptotrachela* (Ren. & Card.) Broth.
9,10 *Pohlia drummondii* (C. Müll.) Andr.
11 *Pohlia filum* (Schimper) Mårt.
12,13 *Pohlia andrewsii* J. Shaw.

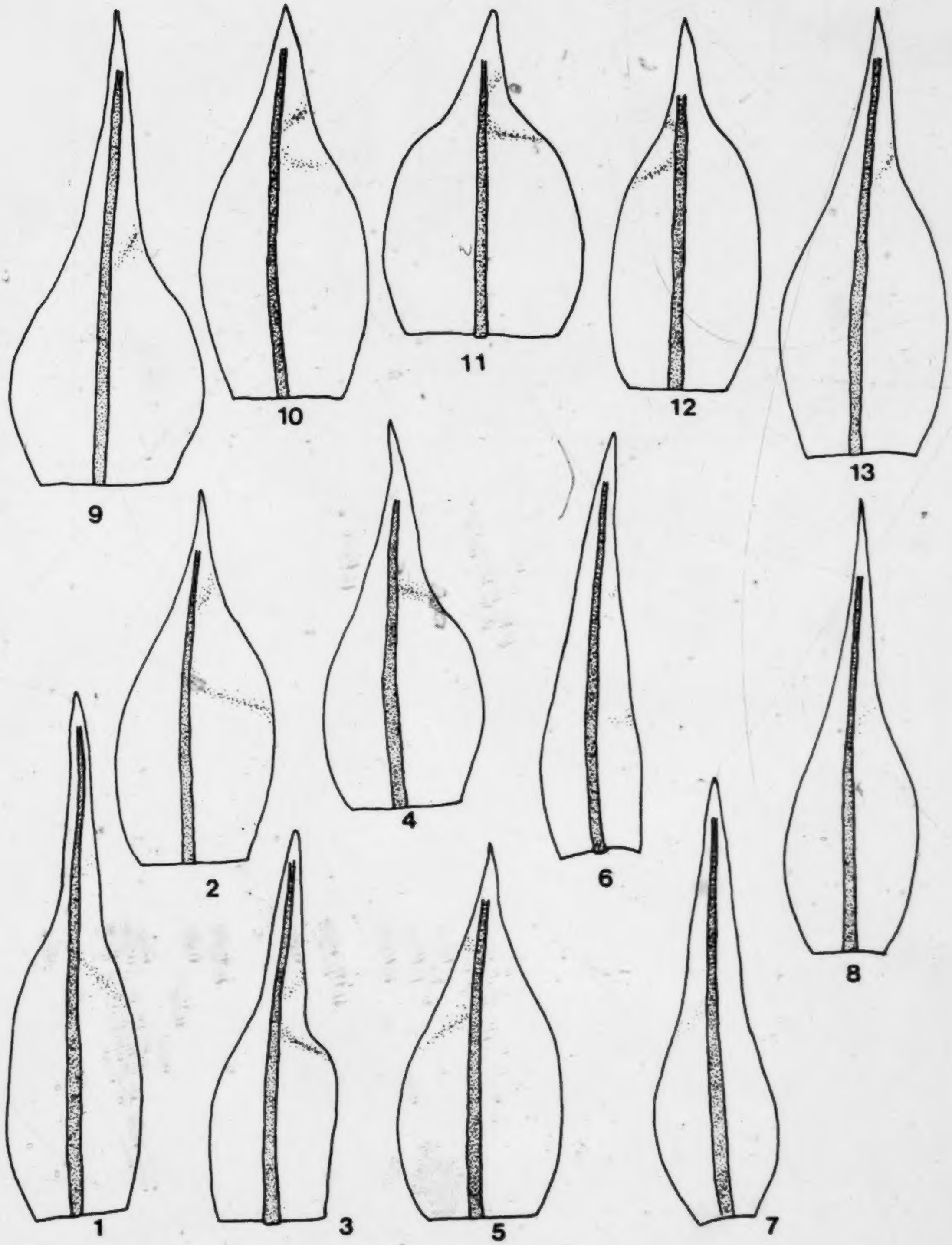
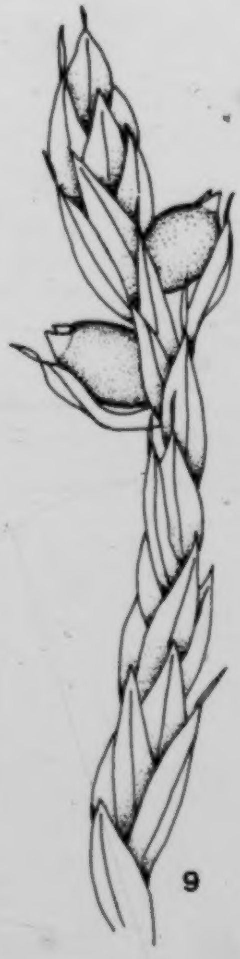


FIGURE 5. Comparison of habit and propagulum morphology in *P. andalusica* (Höhnel) Broth. and *P. filum* (Schimper) Mårt.

1-4 *Pohlia andalusica*, range of variation in propagulum morphology sometimes found in one population (x288)
5 *Pohlia andalusica*, habit (x10)
6-8 *Pohlia filum*, variation in propagulum morphology (x288)
9 *Pohlia filum*, habit (x10).



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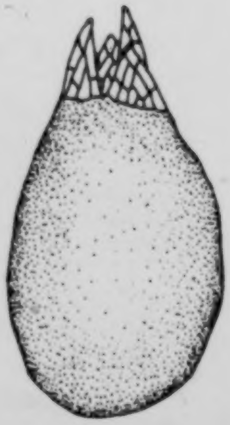

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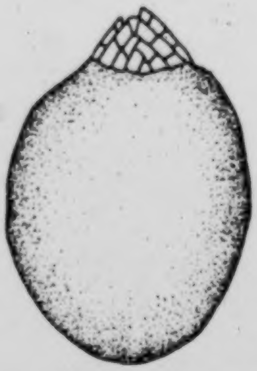

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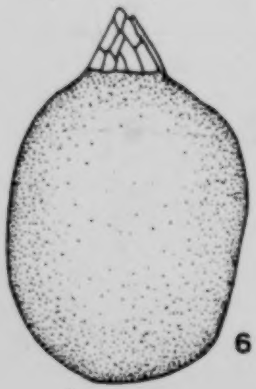

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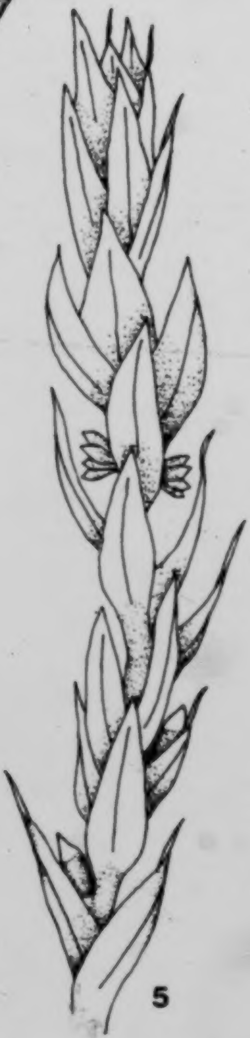

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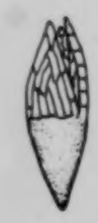

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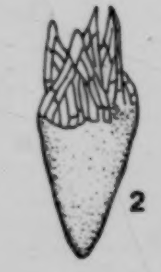

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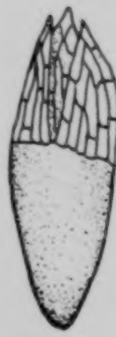

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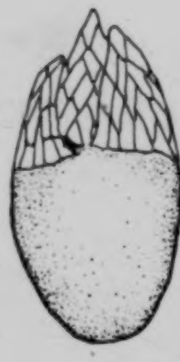

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FIGURE 6. Propagulum morphology

1-8 *Pohlia annotina* (Hedw.) Lindb. (x288)

9-12 *Pohlia camptotrachela* (Ren. & Card.) Broth. (x288)

13-18 *Pohlia proligera* (Lindb. *ex* Breidl.) Lindb. *ex* Arn. (x288)

19-21 *Pohlia andrewsii* J. Shaw (x288)

22 *Pohlia drummondii* (C. Müll.) Andr., sterile shoot grown in moist culture showing abnormal development of propagula as axillary branches (x8)

23 *Pohlia annotina* (Hedw.) Lindb., clustered propagula at early developmental stage (x227).

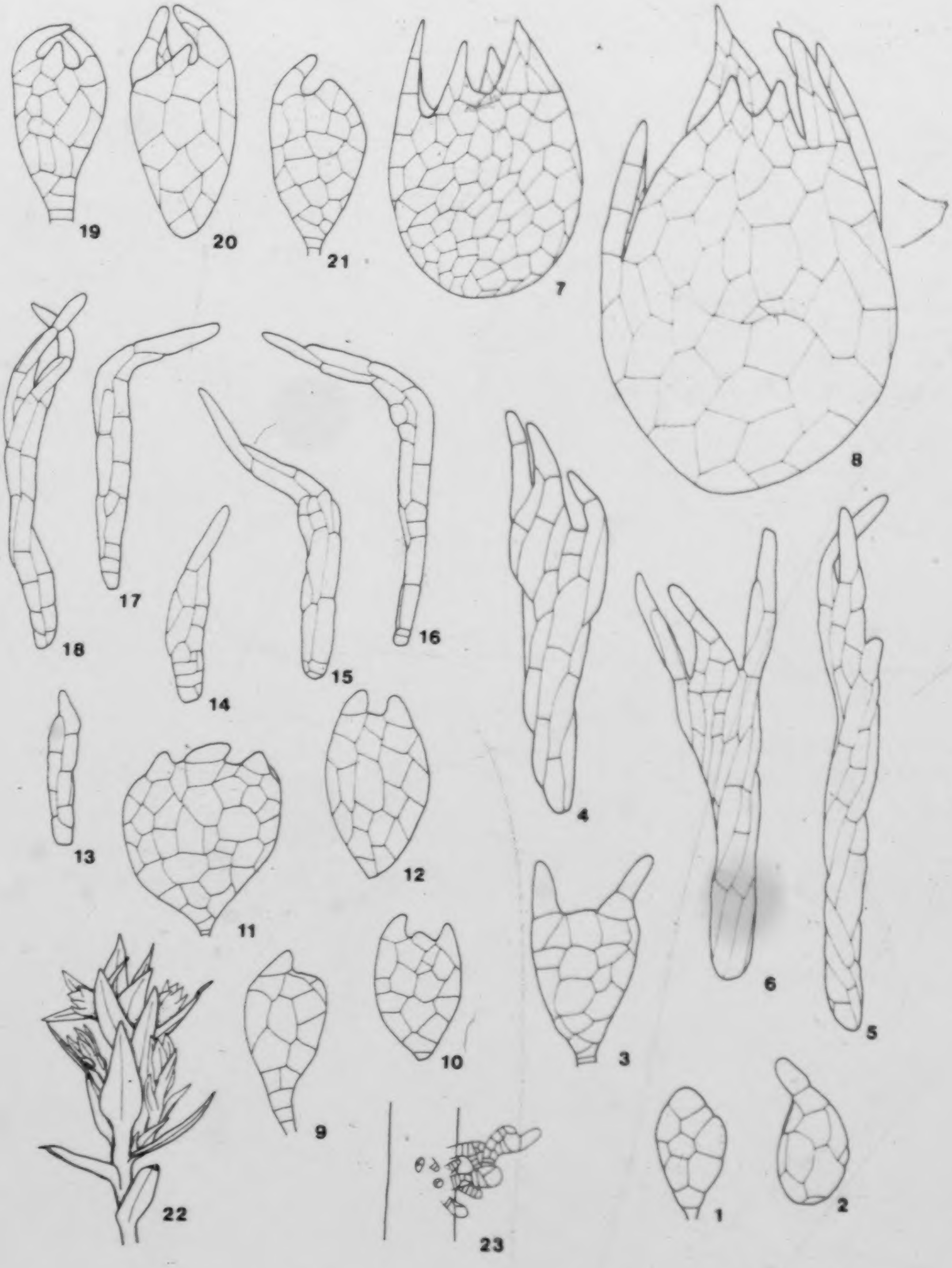

FIGURE 7. Propagulum morphology (x121)
1-4 *Pohlia tundrae* J. Shaw
5,6 *Pohlia bulbifera* (Warnst.) Warnst.
7-9 *Pohlia andalusica* (Höhnel) Broth.
10-13 *Pohlia drummondii* (C. Müll.) Andr.
15-17 *Pohlia filum* (Schimper) Mårt.

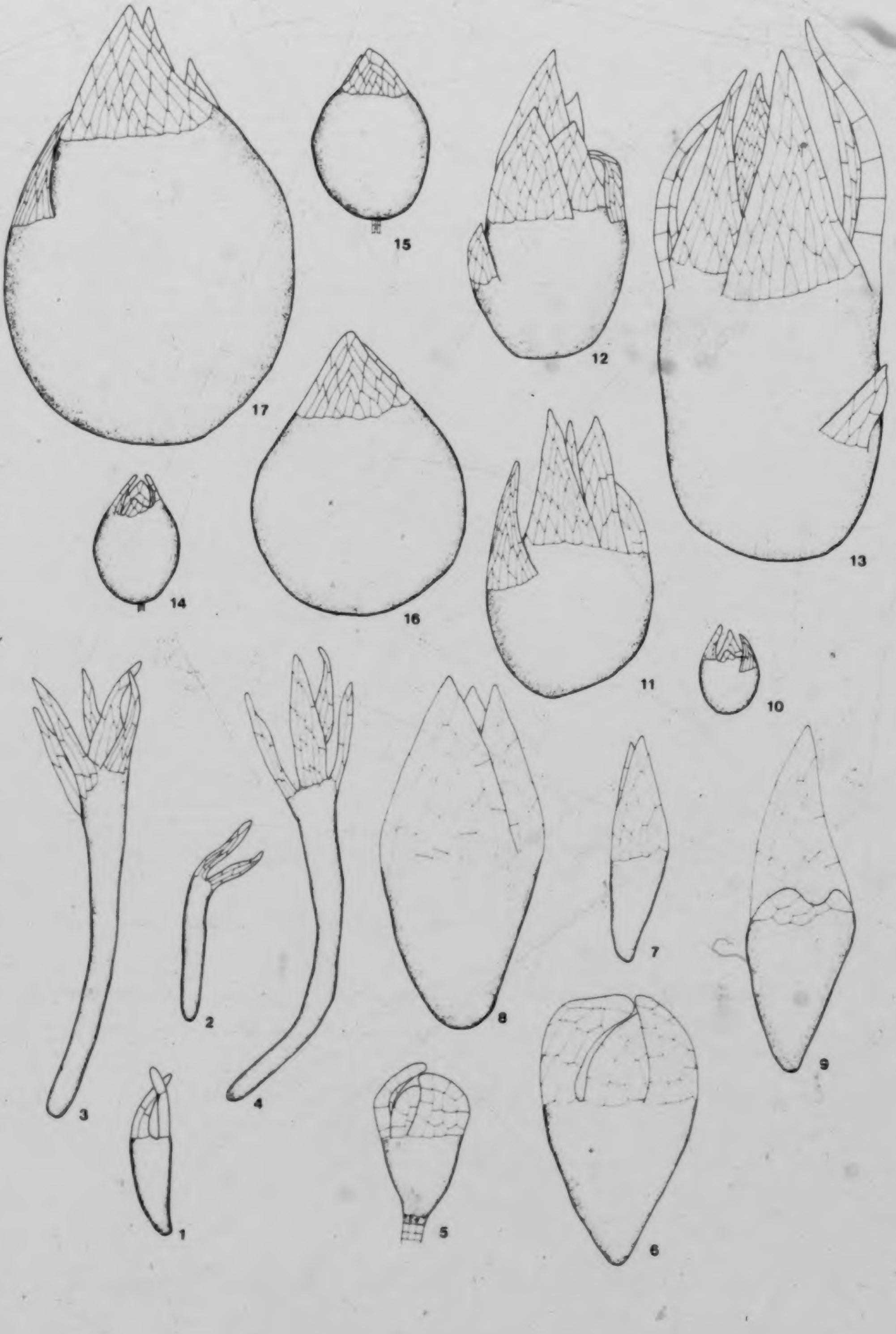

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FIGURE 8. Phylogeny as progressive ontogenetic modification. Modified from Foster and Gifford (1974).

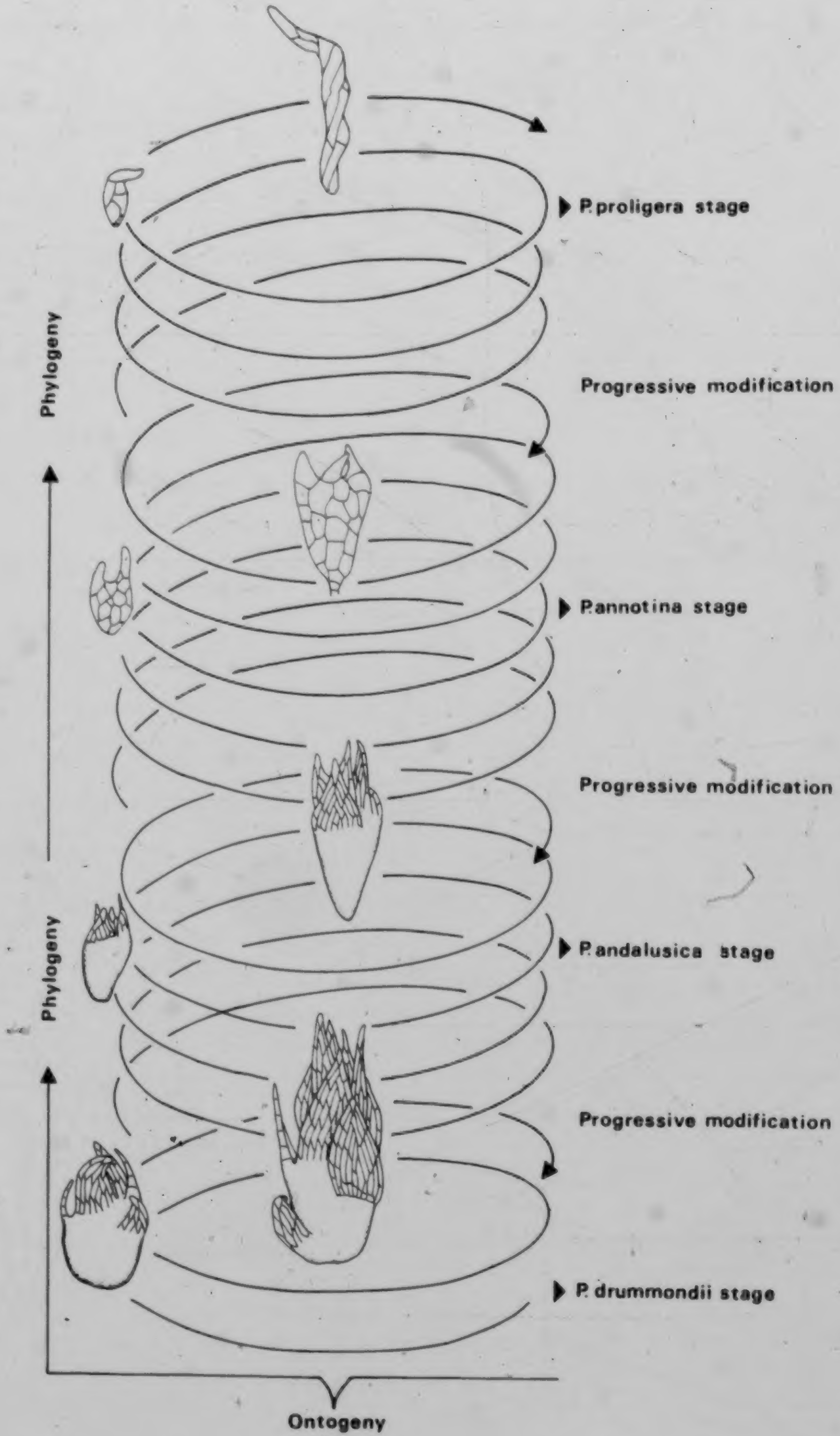

P. proligera stage
Progressive modification
P. annotina stage
Progressive modification
P. andalusica stage
Progressive modification
P. drummondii stage
Phylogeny
Phylogeny
Ontogeny

FIGURE 9. Annuli, peristome, stomata, opercula

1 *Pohlia tundrae* J. Shaw, annulus (x390)

2 *Pohlia drummondii* (C. Müll.) Andr., annulus (x390)

3 *Pohlia andrewsii* J. Shaw, annulus (x390)

4 *Pohlia proligera* (Lindb. *ex* Breidl.) Lindb. *ex* Arn., annulus (x390)

5 *Pohlia annotina* (Hedw.) Lindb., annulus (x390)

6 *Pohlia camptotrachela* (Ren. & Card.) Broth., annulus (x390)

7 *Pohlia camptotrachela* (Ren. & Card.) Broth., peristome (x288)

8-10 *Pohlia tundrae* J. Shaw, three stomates from one capsule (x390)

11-13 *Pohlia andalusica* (Höhnel) Broth., exostome teeth, transverse section (x390)

14 *Pohlia obtusifolia* (Brid.) L. Koch, operculum, dry (x36)

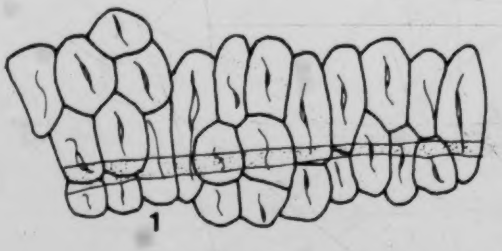
15 *Pohlia obtusifolia* (Brid.) L. Koch, operculum, moist (x36)

16 *Pohlia drummondii* (C. Müll.) Andr., operculum, dry (x36)

17 *Pohlia drummondii* (C. Müll.) Andr., operculum, moist (x36)

18 *Pohlia annotina* (Hedw.) Lindb. operculum, dry (x36)

19 *Pohlia annotina* (Hedw.) Lindb. operculum, moist (x36).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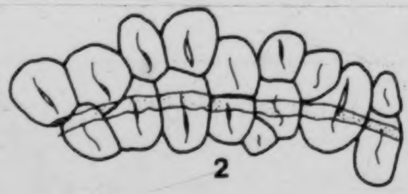
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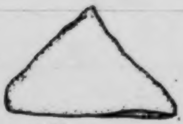
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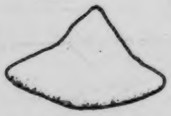
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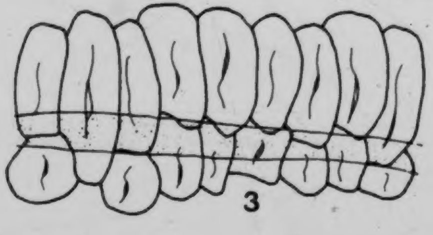
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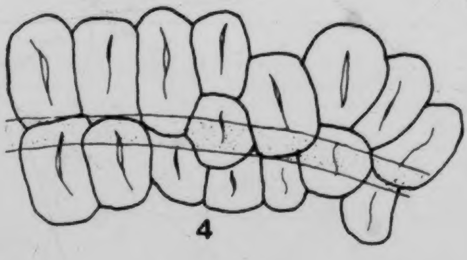
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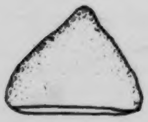
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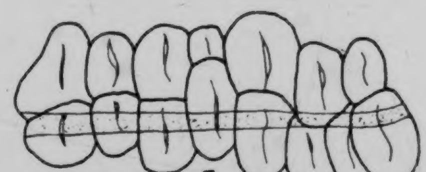
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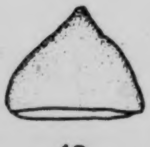
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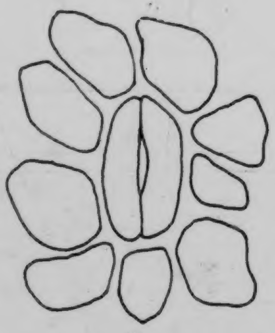
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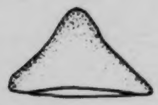
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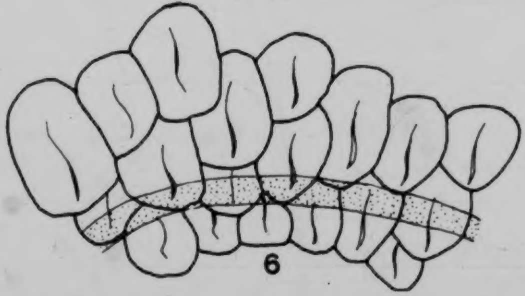
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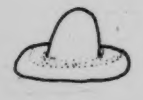
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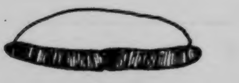
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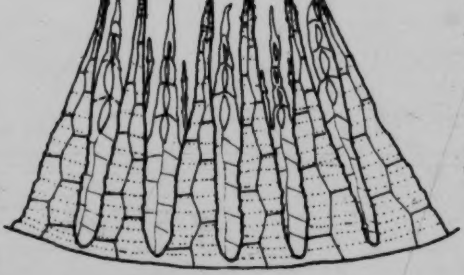
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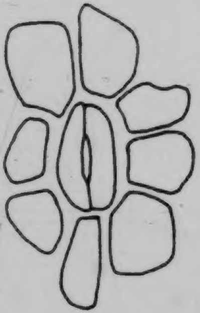
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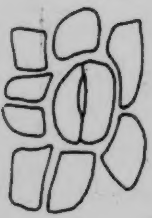
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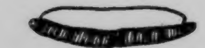
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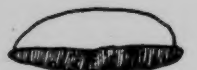

11

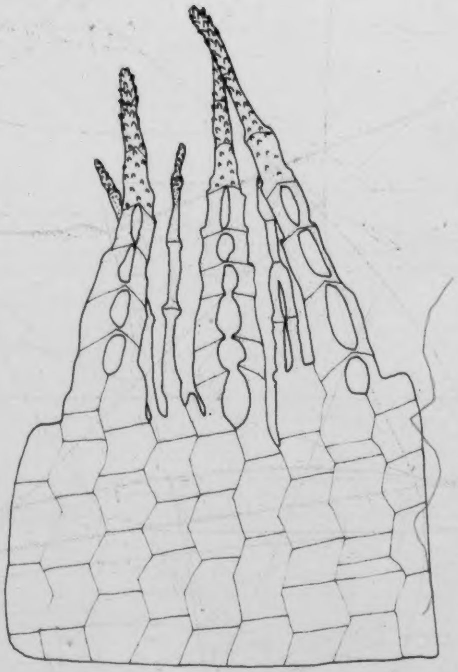
FIGURE 10. Exostome, endostome, exothecial cells

1 *Pohlia andrewsii* J. Shaw, exothecial cells where capsule attaches to seta (x390)

2 *Pohlia tundrae* J. Shaw, exothecial cells of urn (x390)

3 *Pohlia annotina* (Hedw.) Lindb., exothecial cells at capsule rim (x390)

4-7 *Pohlia drummondii* (C. Müll.) Andr. 4-endostome, 5-exostome tooth, dorsal surface, 6-exostome tooth, ventral surface, 7-exostome tooth, longitudinal section (x374)



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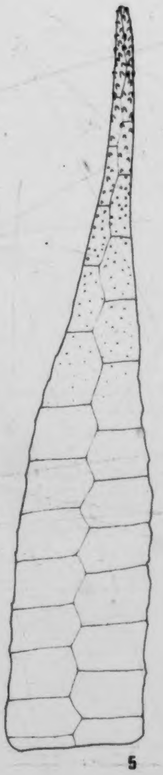

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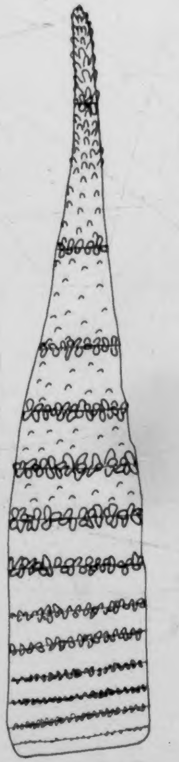

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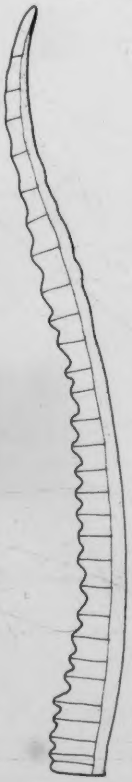

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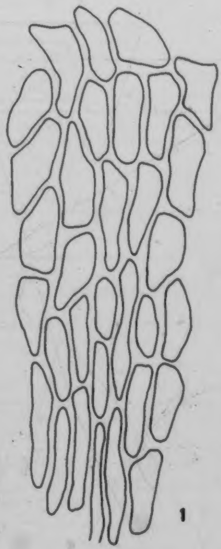

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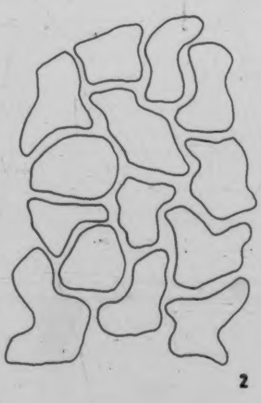

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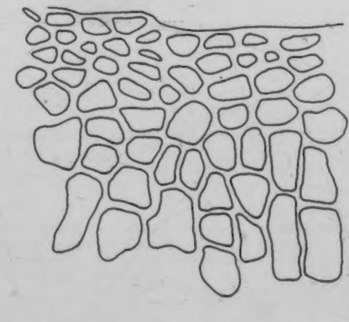


3

FIGURE 11. SEM photographs of propagula and leaf surface

1 *Pohlia proligera* (Lindb. *ex* Breidl.) Lindb. *ex* Arn., adaxial leaf surface showing cuticle-like layer (x350)

2 *Pohlia camptotrachela* (Ren. & Card.) Broth., propagulum, showing spiral arrangement of peglike leaf primordia (x450)

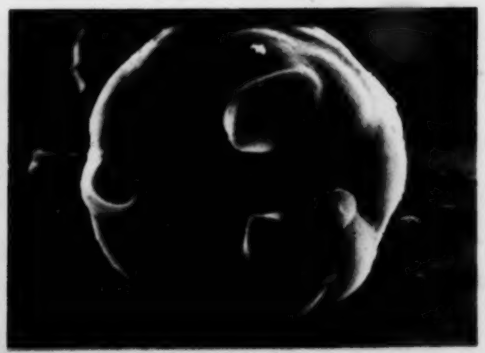
3 *Pohlia filum* (Schimper) Mart., propagulum, showing spiral arrangement of laminal leaf primordia (x120)

4 *Pohlia drummondii* (C. Mull.) Andr., propagulum (x80)

5 *Pohlia filum* (Schimper) Mart., propagulum (x80)

6 *Pohlia bulbifera* (Warnst.) Warnst., propagulum, showing bulging superficial cells and concave, laminal leaf primordia (x70)

1



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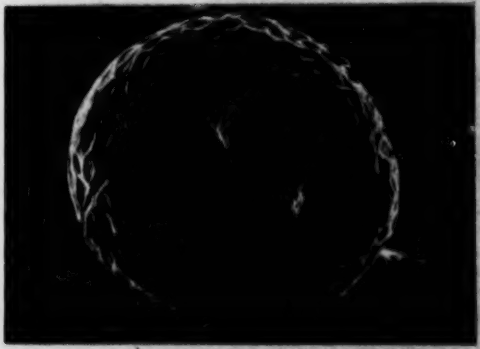

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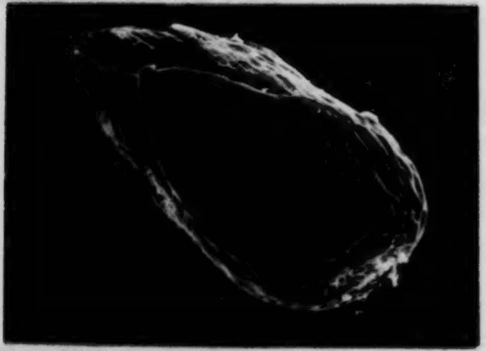

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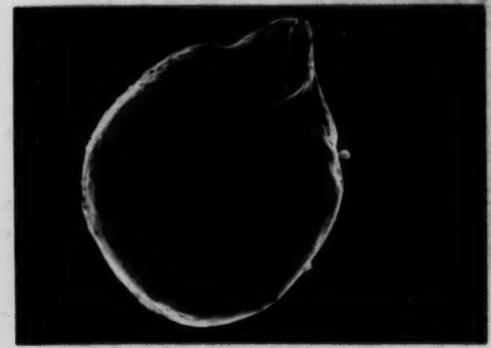

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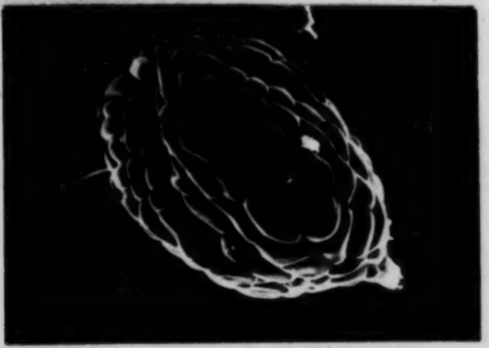
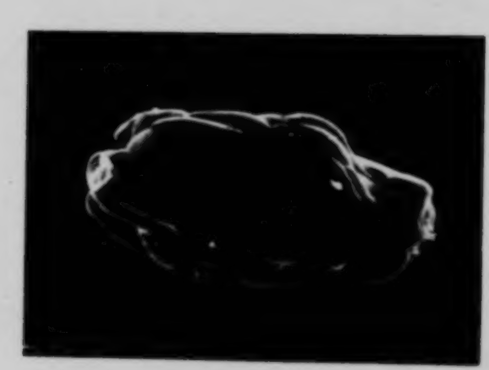


6

FIGURE 12.

1 *Pohlia andrewsii* J. Shaw, propagulum, showing short, peglike, incurved leaf primordia (x300)
2 *Pohlia annotina* (Hedw.) Lindb., propagulum, showing erect, peglike leaf primordia (x300)
3 *Pohlia tundrae* J. Shaw, propagulum, showing apical and subapical, laminal leaf primordia (x80)
4 *Pohlia drummondii* (C. Müll.) Andr., spore (x2750)
5 *Pohlia filum* (Schimper) Mårt., spore (x2750)
6 *Pohlia andalusica* (Höhnel) Broth. (x2750)



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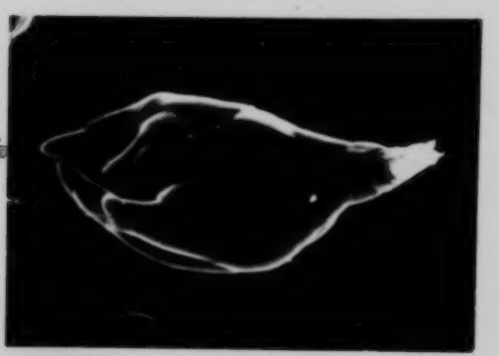

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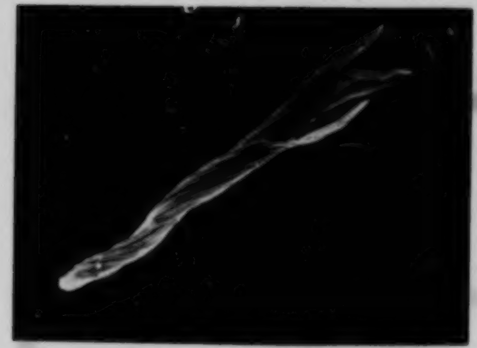

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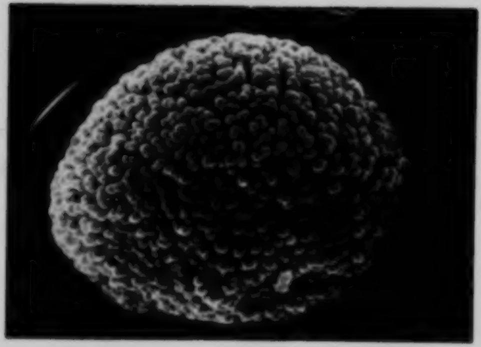

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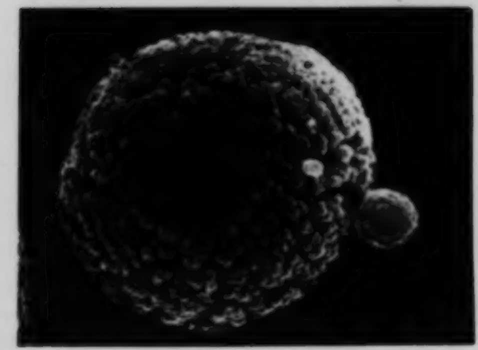

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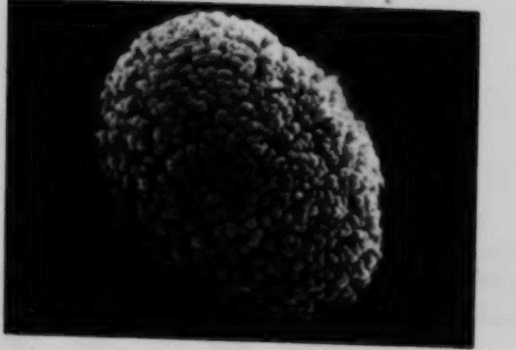
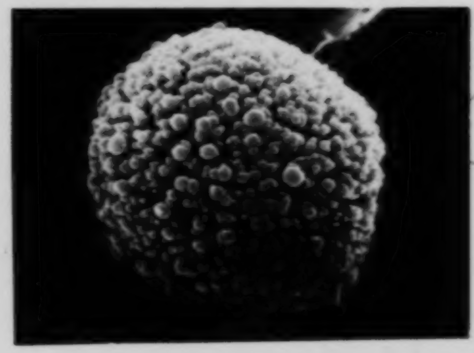


6

FIGURE 13. SEM photographs of spores

1 *Pohlia tundrae* J. Shaw (x2750)
2 *Pohlia bulbifera* (Warnst.) Warnst. (x2750)
3 *Pohlia andrewsii* J. Shaw (x2750)
4 *Pohlia annotina* (Hedw.) Lindb. (x2750)
5 *Pohlia proligera* (Lindb. *ex* Kindb. *ex* Breidl.) Arn. (x2750)
6 *Pohlia camptotrachela* (Ren. & Card.) Broth. (x2750)



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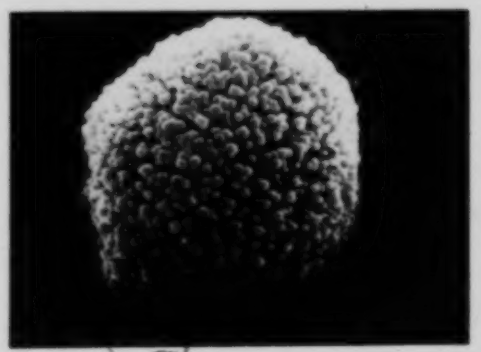

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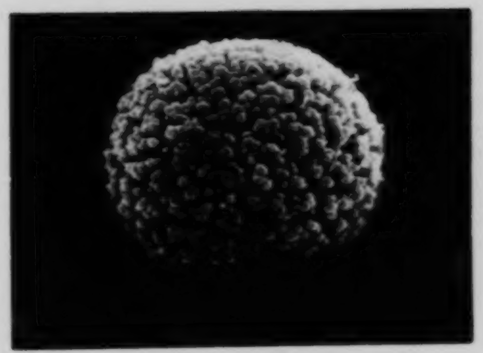

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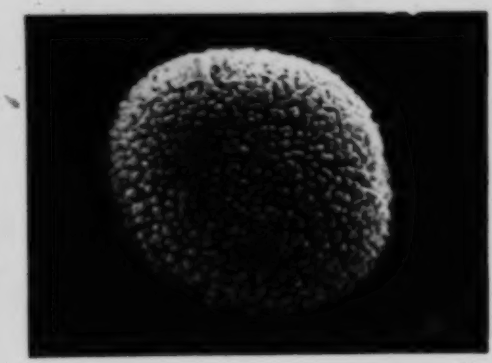

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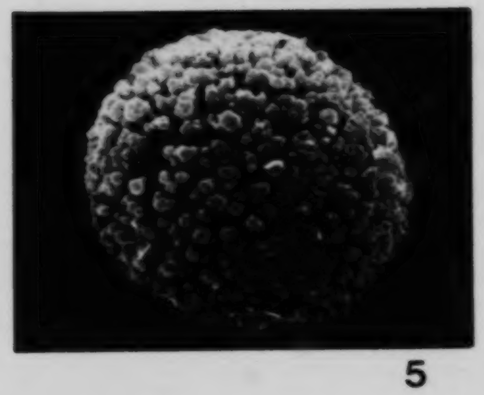


5

6

FIGURE 14. Range of propagulum types probably included in the late eighteenth-early nineteenth century concept of "*Pohlia (Bryum) annotina*"

1-4	*Pohlia annotina* (Hedw.) Lindb.
5	*Pohlia andalusica* (Höhnel) Broth.
6-8	*Pohlia annotina* (Hedw.) Lindb.
9	*Pohlia andalusica* (Höhnel) Broth.
10	*Pohlia bulbifera* (Warnst.) Warnst.
11	*Pohlia andalusica* (Höhnel) Broth.
12	*Pohlia annotina* (Hedw.) Lindb.
13	*Pohlia andalusica* (Höhnel) Broth.
14	*Pohlia filum* (Schimper) Mart.
15	*Pohlia annotina* (Hedw.) Lindb.
16	*Pohlia andalusica* (Höhnel) Broth.
17	*Pohlia drummondii* (C. Müller) Andr.
18	*Pohlia andalusica* (Höhnel) Broth.

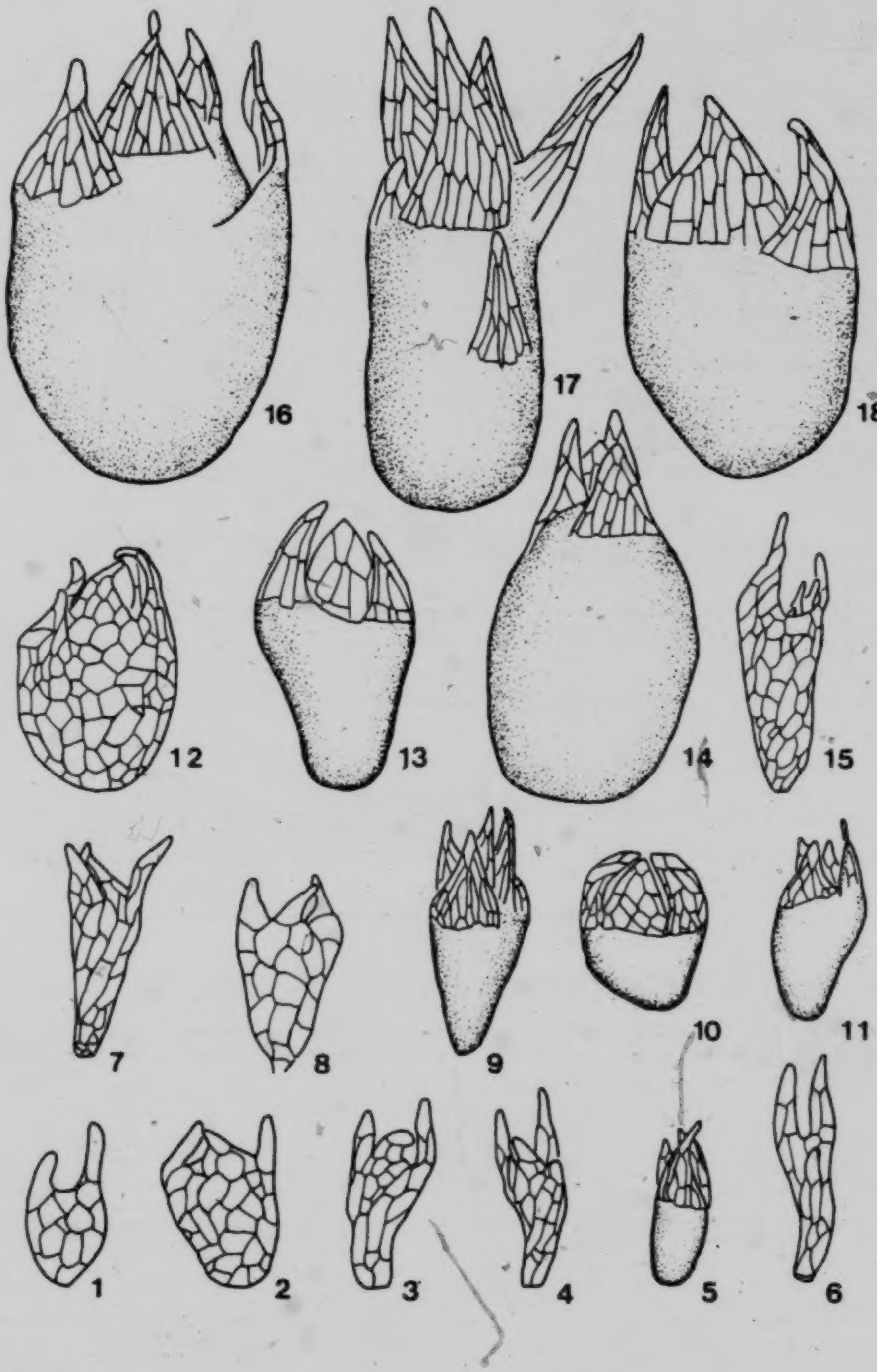


FIGURE 15. Means, standard errors (solid black bars) and standard deviations (hollow bars) of propaguliferous species along the pH gradient

1 *Pohlia proligera* (Lindb. *ex* Breidl.) Lindb. *ex* Arn.
2 *Pohlia filum* (Schimper) Mårt.
3 *Pohlia andalusica* (Höhnel) Broth.
4 *Pohlia drummondii* (C. Müll.) Andr.
5 *Pohlia tundrae* J. Shaw
6 *Pohlia camptotrachela* (Ren. & Card.) Broth.
7 *Pohlia annotina* (Hedw.) Lindb.

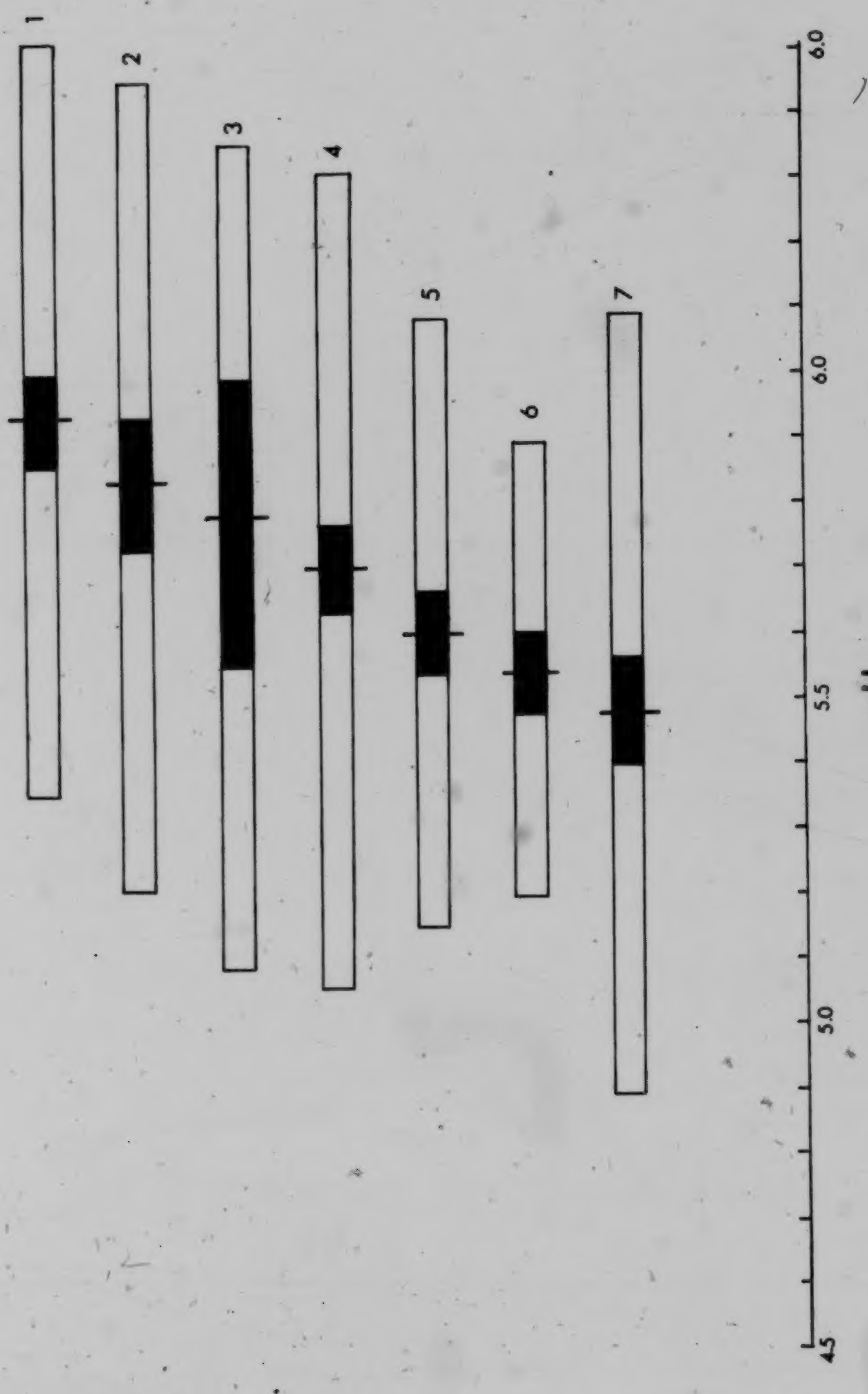

1
2
3
4
5
6
7
4.5
5.0
5.5
6.0
6.0
pH

FIGURE 16. Means, standard errors (solid black bars) and standard deviations (hollow black bars) of propaguliferous species along the organic matter gradient

1 *Pohlia tundrae* J. Shaw
2 *Pohlia drummondii* (C. Müll.) Andr.
3 *Pohlia andalusica* (Höhnel) Broth.
4 *Pohlia proligera* (Lindb. *ex* Breidl.) Lindb. *ex* Arn.
5 *Pohlia annotina* (Hedw.) Lindb.
6 *Pohlia camptotrachela* (Ren. & Card.) Broth.
7 *Pohlia filum* (Schimper) Mart.

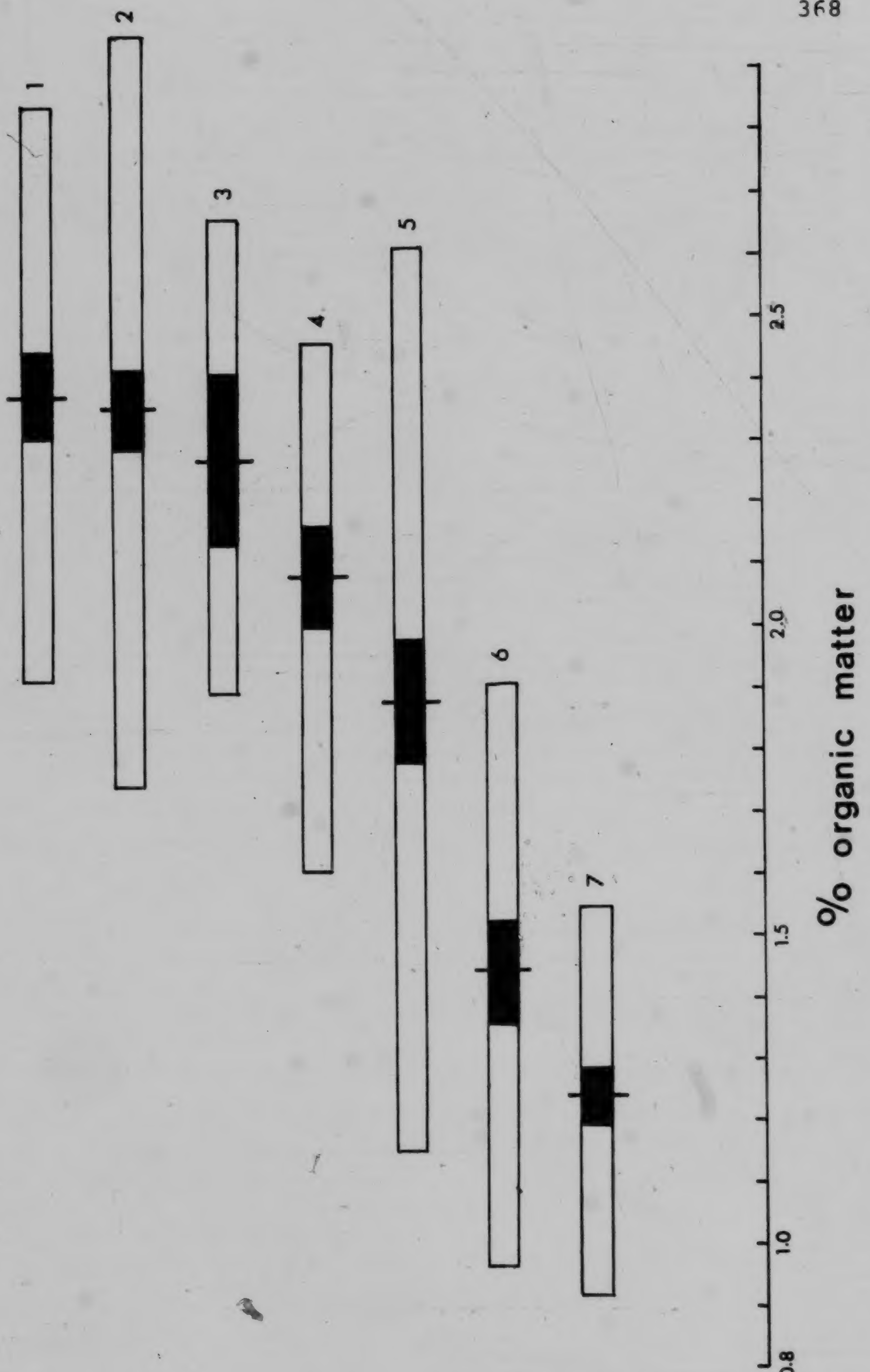
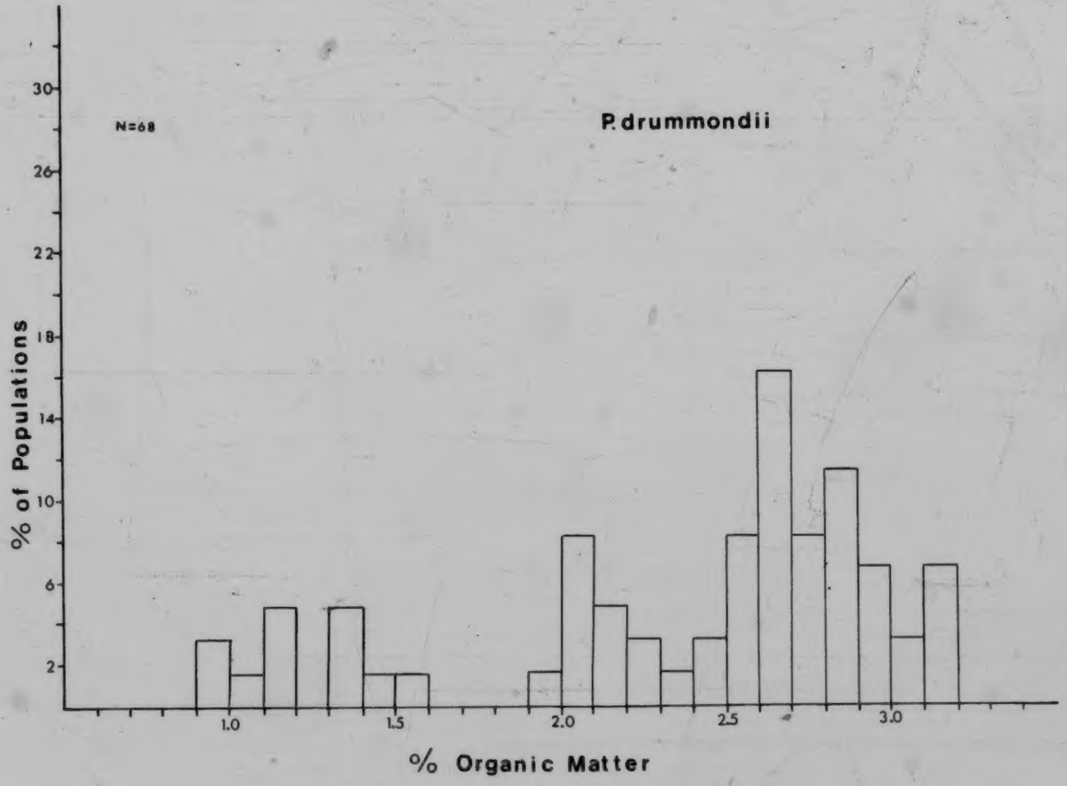

1
2
3
4
5
6
7
0.8
1.0
1.5
2.0
2.5
% organic matter

FIGURE 17. *Pohlia drummondii* (C. Müll.) Andr., histograms of resource utilization along organic matter and pH gradients.


N=68
P. drummondii
% of Populations
30
26
22
18
14
10
6
2
1.0
1.5
2.0
2.5
3.0
% Organic Matter

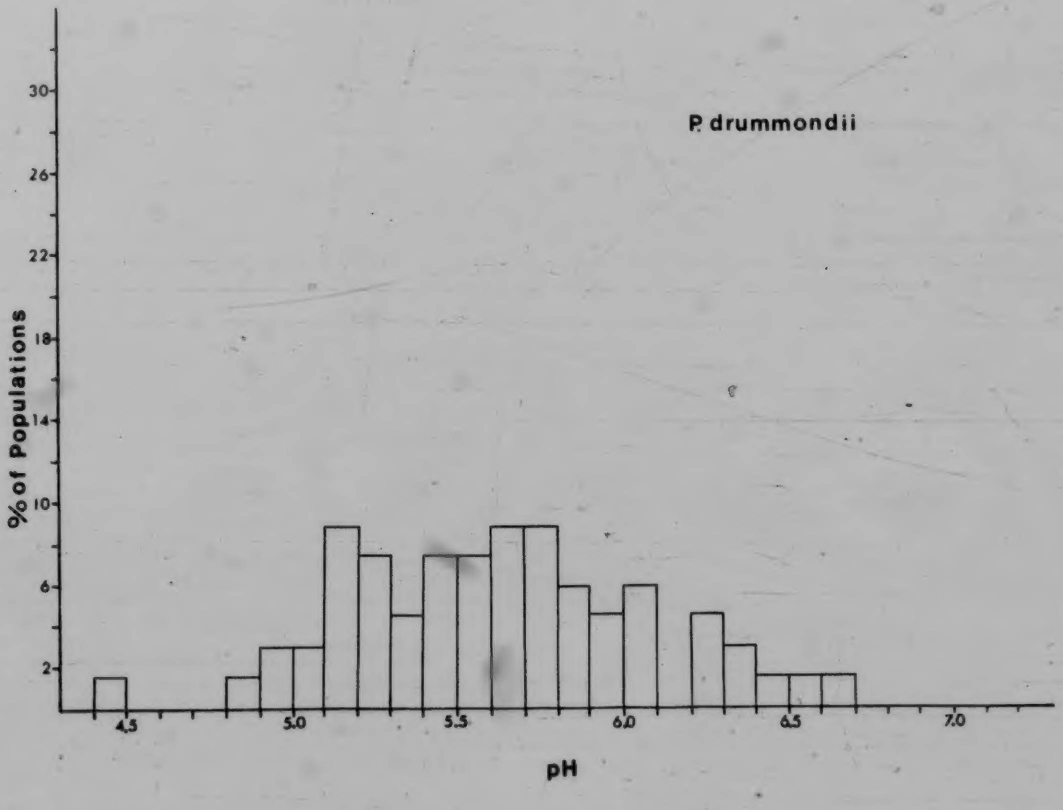

P. drummondii
% of Populations
30
26
22
18
14
10
6
2
4.5
5.0
5.5
6.0
6.5
7.0
pH

FIGURE 18. *Pohlia drummondii* (C. Müll.) Andr., resource utilization along organic matter and pH gradients
outer shaded = 90% of populations
middle strips = 50% of populations
inner black = 20% of populations.

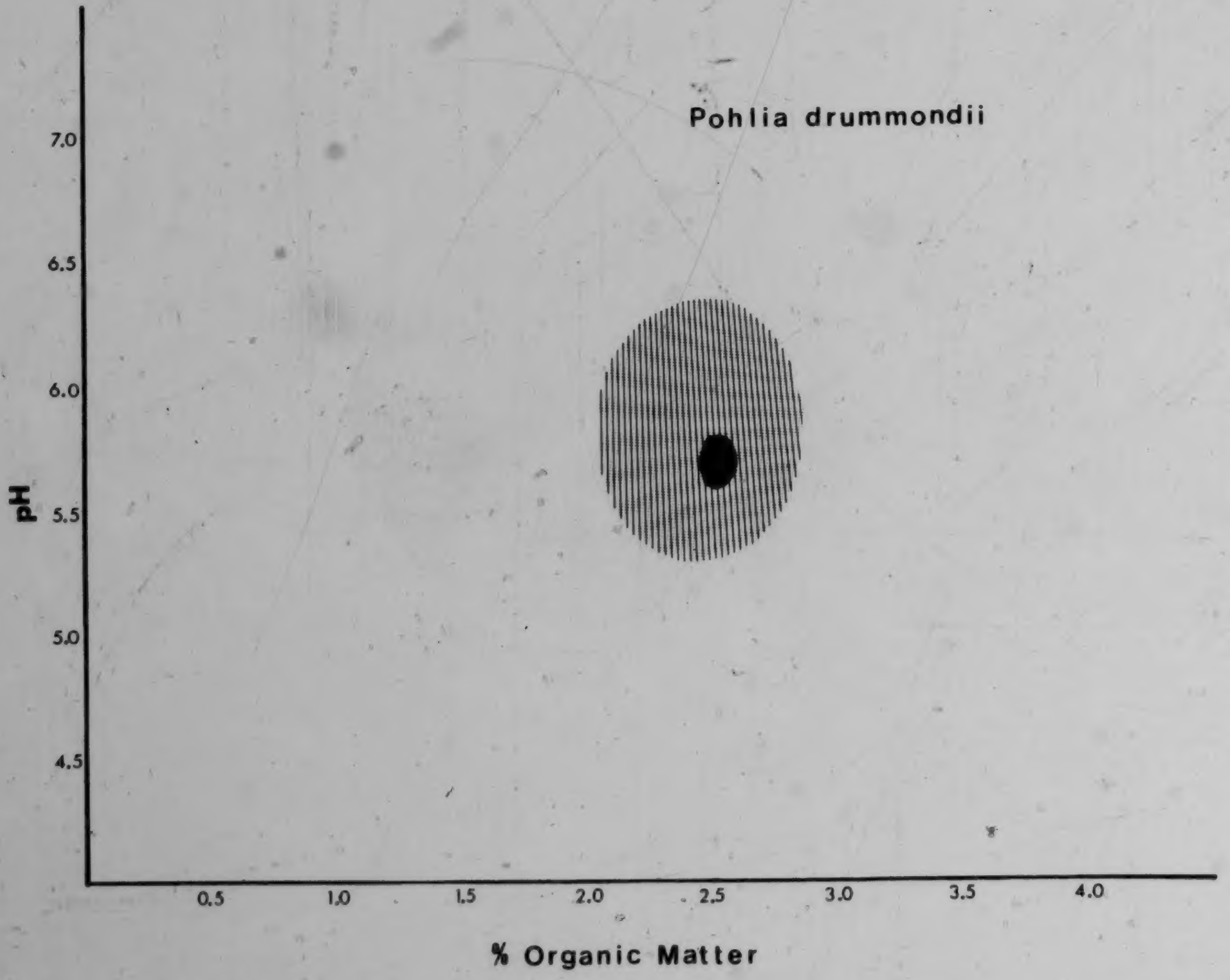
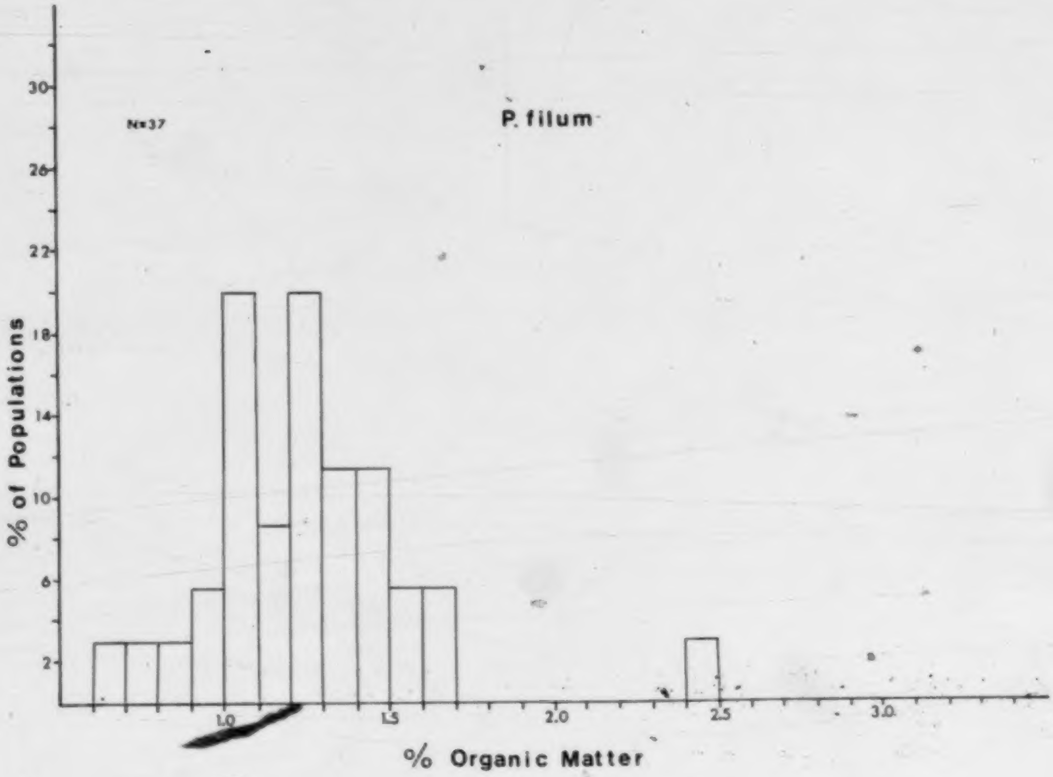

Pohlia drummondii
pH
7.0
6.5
6.0
5.5
5.0
4.5
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
% Organic Matter

FIGURE 19. *Pohlia filum* (Schimper) Mårt., histograms of resource utilization along organic matter and pH gradients.


N=37
P. filum
30
26
22
18
14
10
6
2
% of Populations
1.0
1.5
2.0
2.5
3.0
% Organic Matter

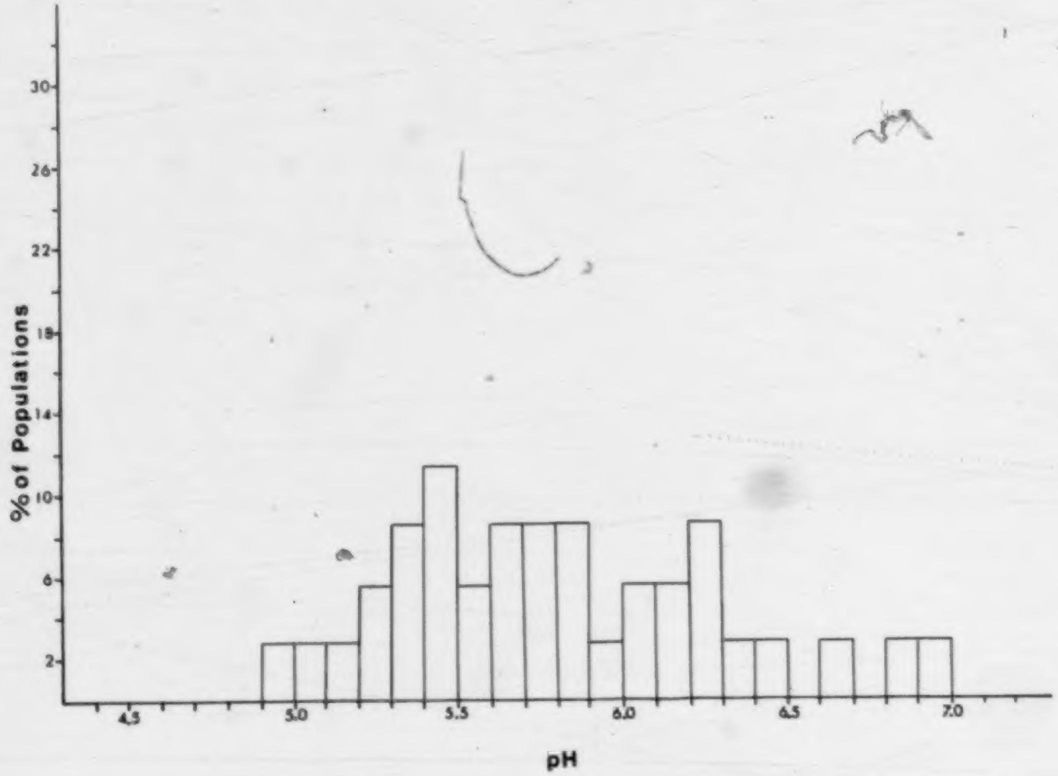

30
26
22
18
14
10
6
2
% of Populations
4.5
5.0
5.5
6.0
6.5
7.0
pH

FIGURE 20. *Pohlia filum* (Schimper) Mårt., resource utilization along organic matter and pH gradients
outer shaded = 90% of populations
middle striped = 50% of populations
inner black = 20% of populations.

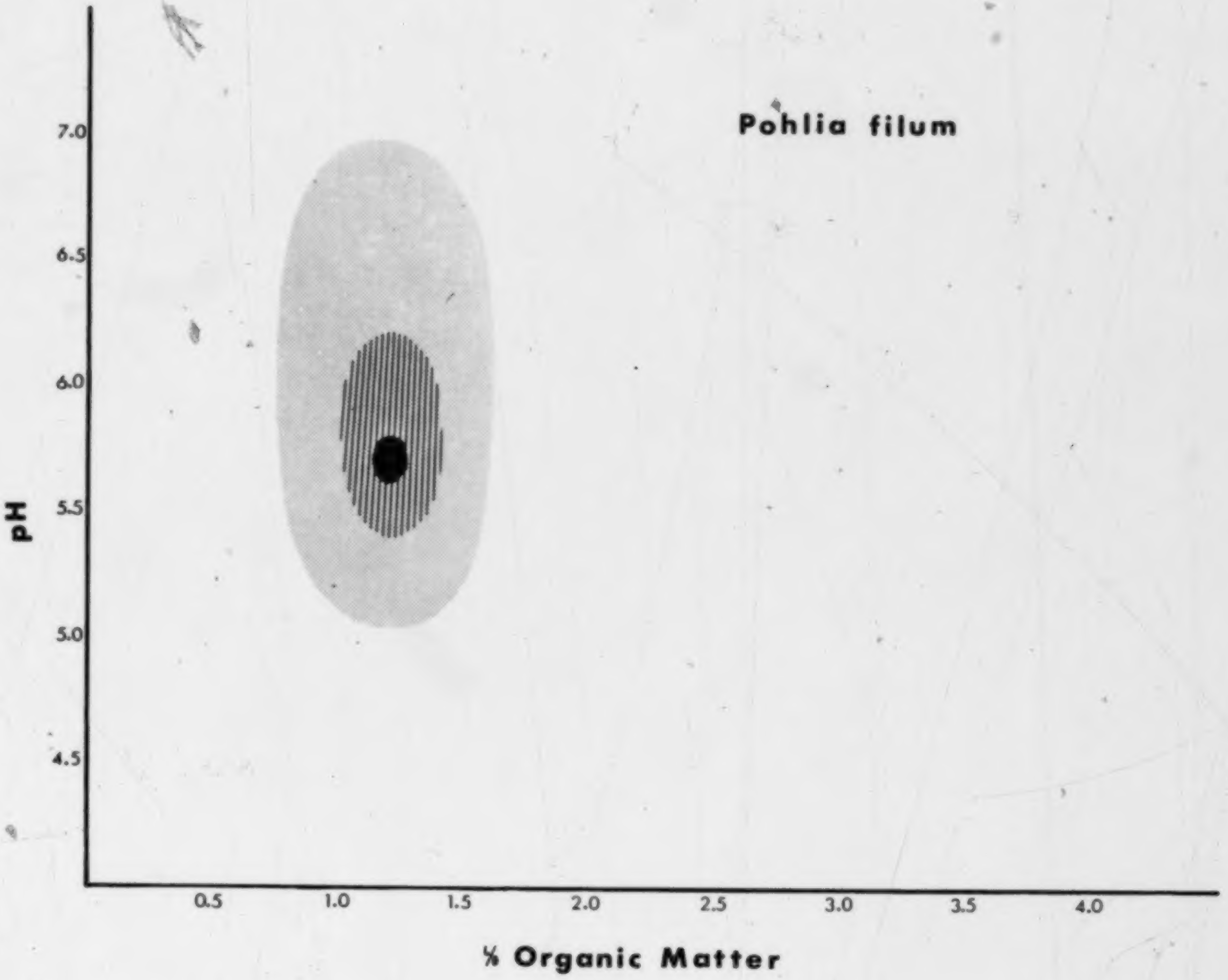
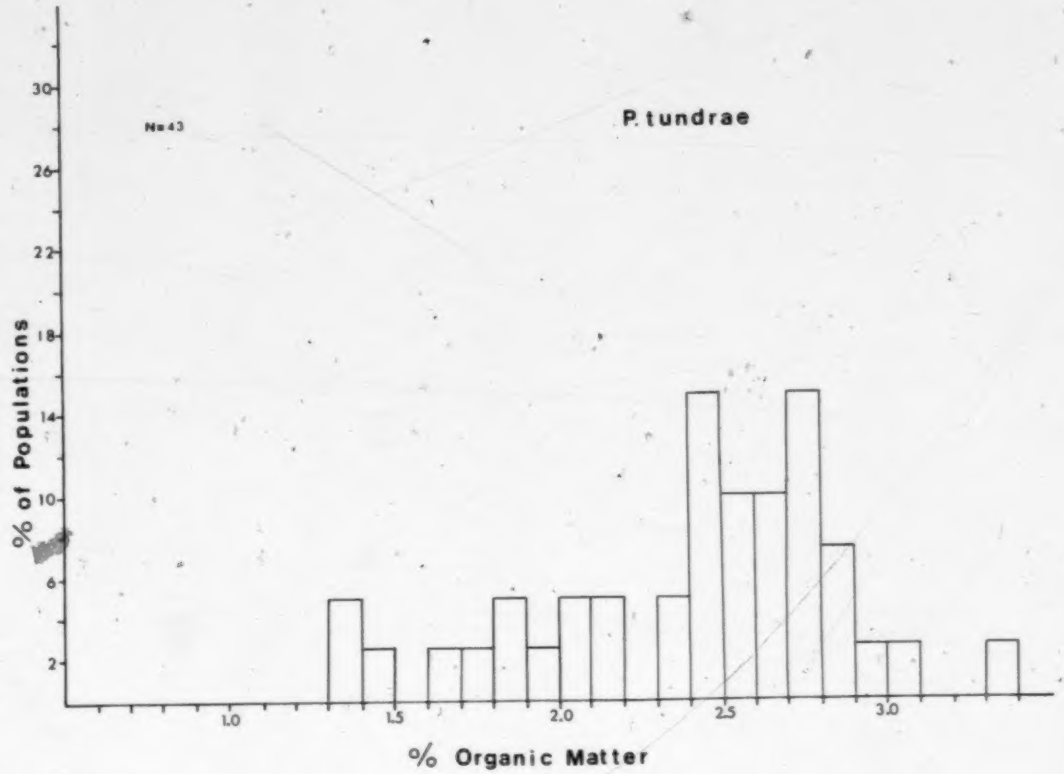

Pohlia filum
pH
7.0
6.5
6.0
5.5
5.0
4.5
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
% Organic Matter

FIGURE 21. *Pohlia tundrae* J. Shaw, histograms of resource utilization along organic matter and pH gradients.


N=43
P. tundrae
% of Populations
30
26
22
18
14
10
6
2
1.0
1.5
2.0
2.5
3.0
% Organic Matter

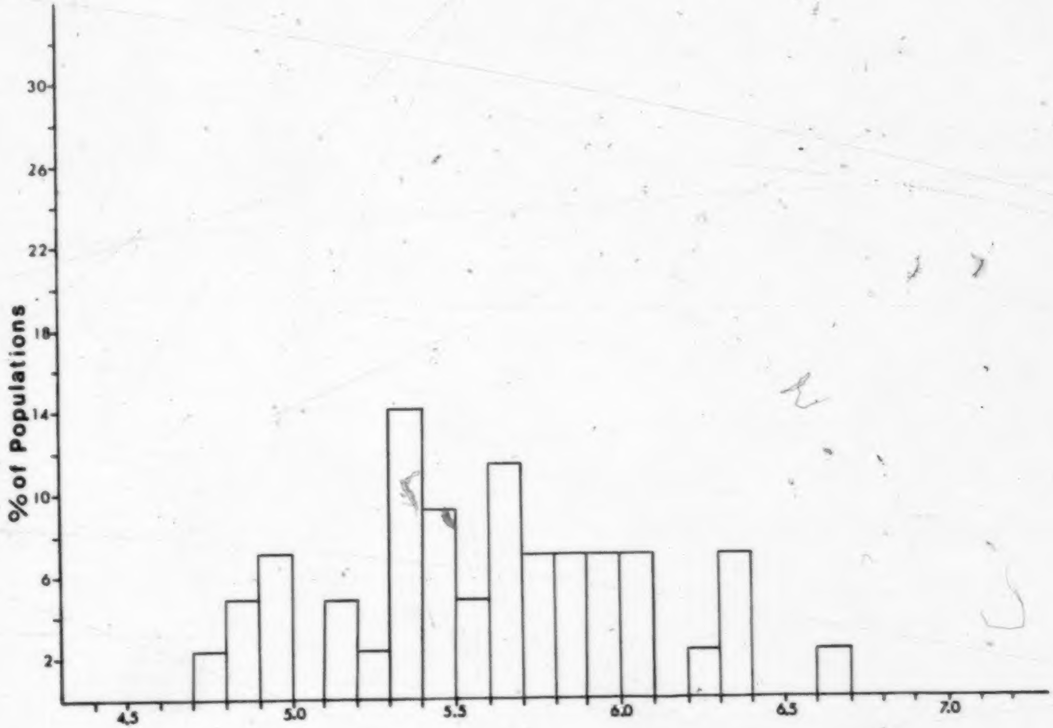

% of Populations
30
26
22
18
14
10
6
2
4.5
5.0
5.5
6.0
6.5
7.0
pH

FIGURE 22. *Pohlia tundrae* J. Shaw, resource utilization along organic matter and pH gradients
outer shaded = 90% of populations
middle striped = 50% of populations
inner black = 20% of populations.

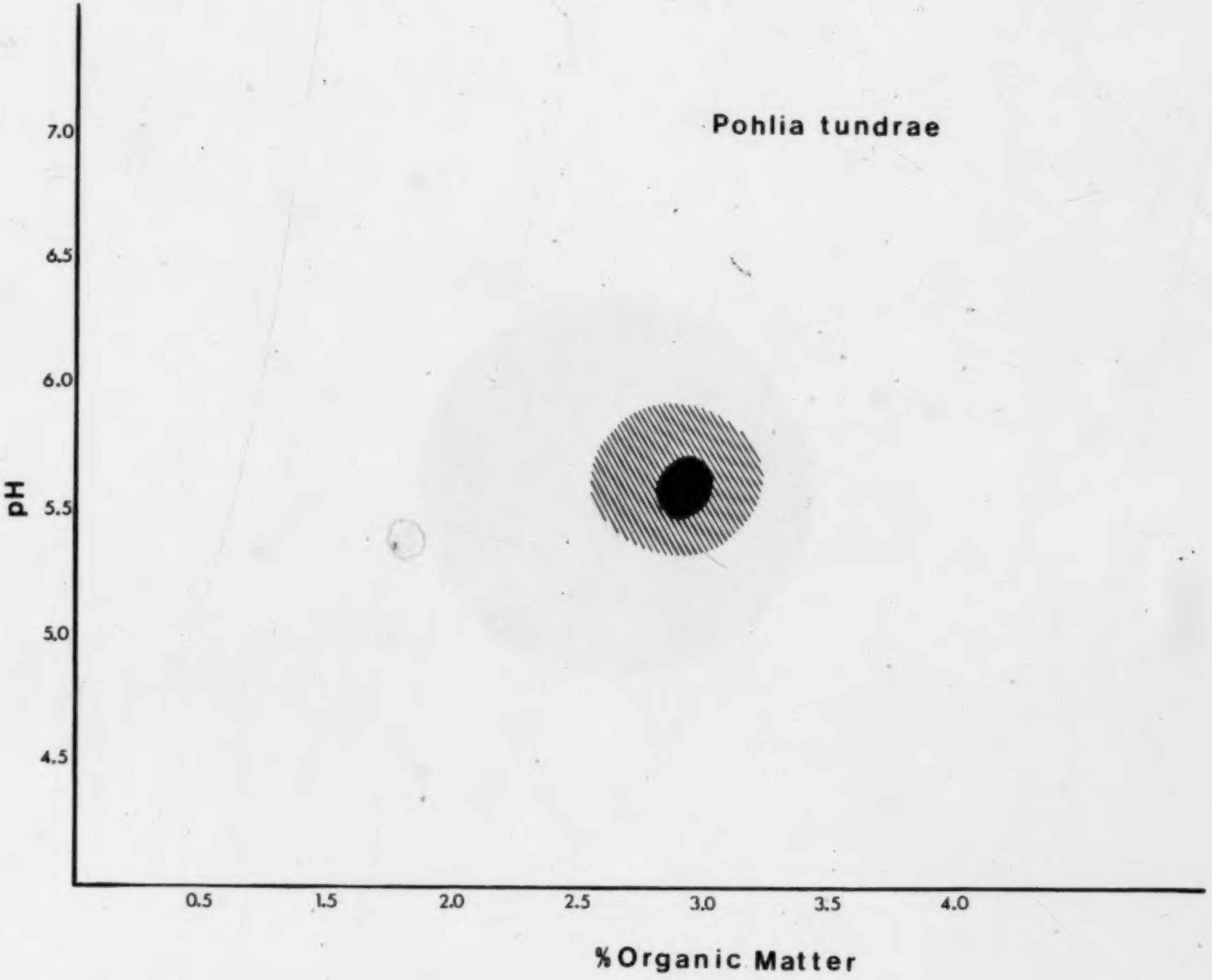
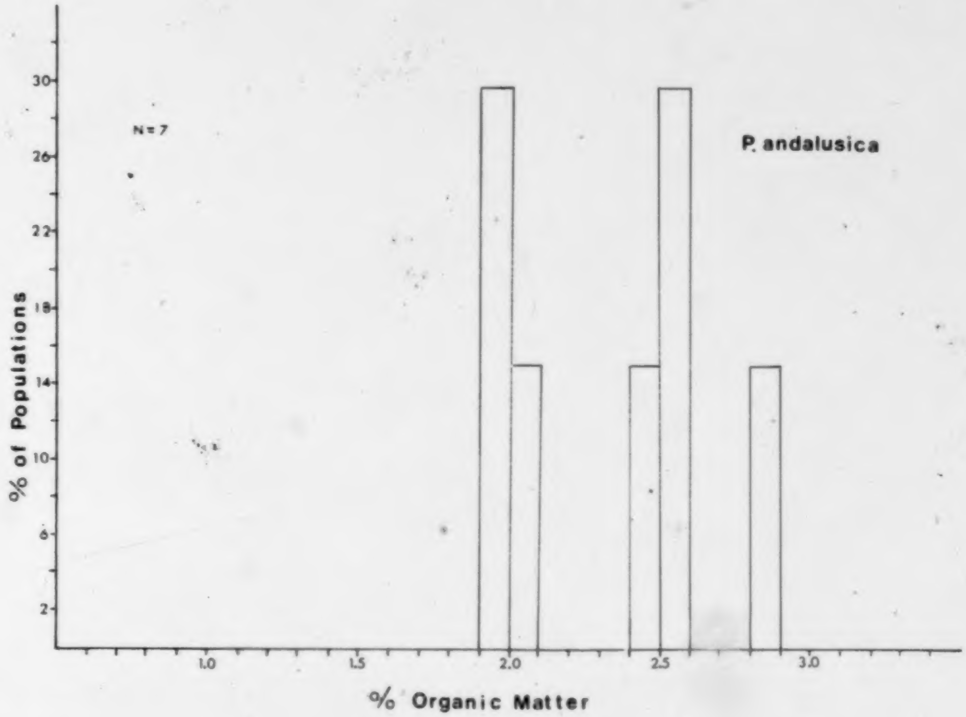

Pohlia tundrae
pH
7.0
6.5
6.0
5.5
5.0
4.5
0.5
1.5
2.0
2.5
3.0
3.5
4.0
%Organic Matter

FIGURE 23. *Pohlia andalusica* (Höhnel) Broth., histograms of resource utilization along organic matter and pH gradients.


N=7
P. andalusica
% of Populations
30
26
22
18
14
10
6
2
1.0
1.5
2.0
2.5
3.0
% Organic Matter

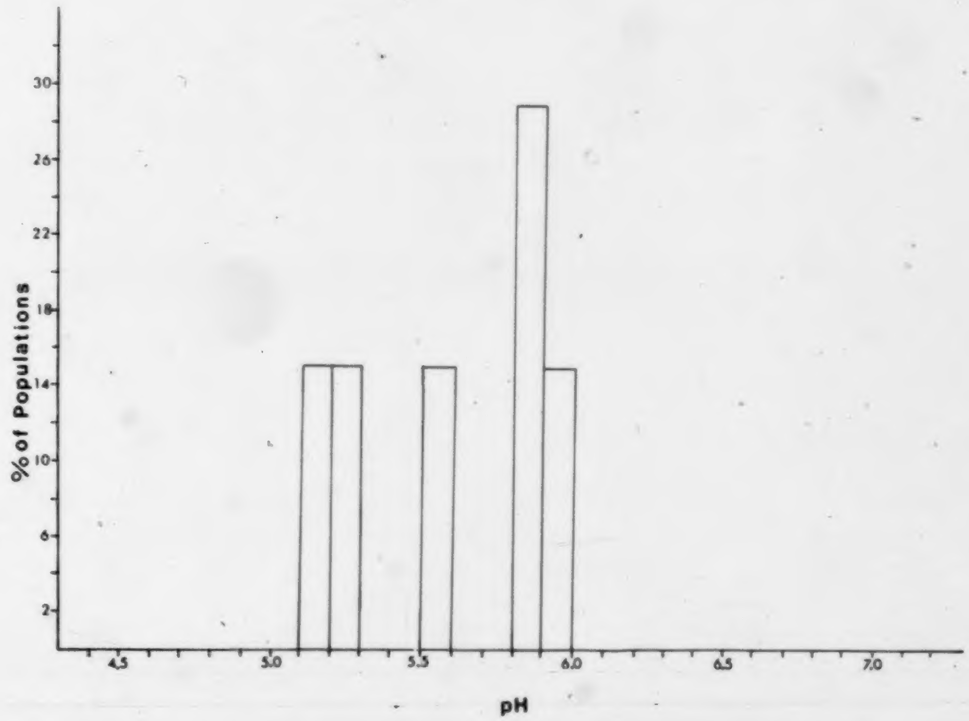
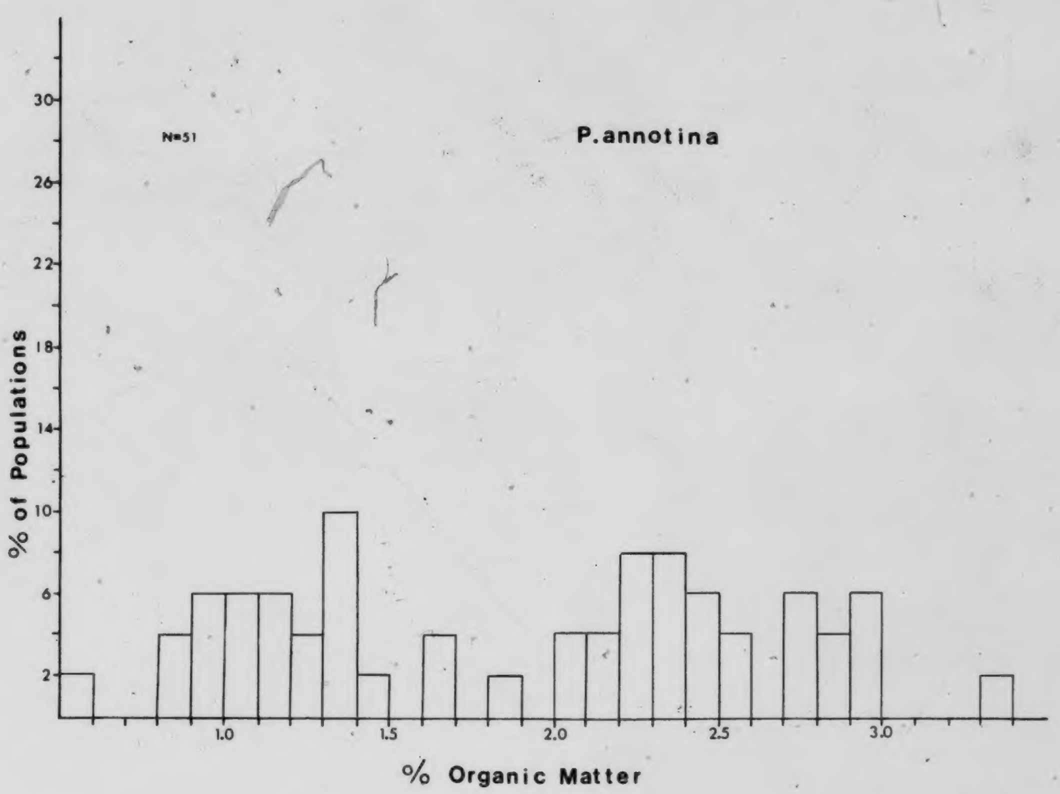

% of Populations
30
26
22
18
14
10
6
2
4.5
5.0
5.5
6.0
6.5
7.0
pH

FIGURE 24. *Pohlia annotina* (Hedw.) Lindb., histograms of resource utilization along organic matter and pH gradients.


30
26
22
18
14
10
6
2
N=51
P.annotina
% of Populations
1.0
1.5
2.0
2.5
3.0
% Organic Matter

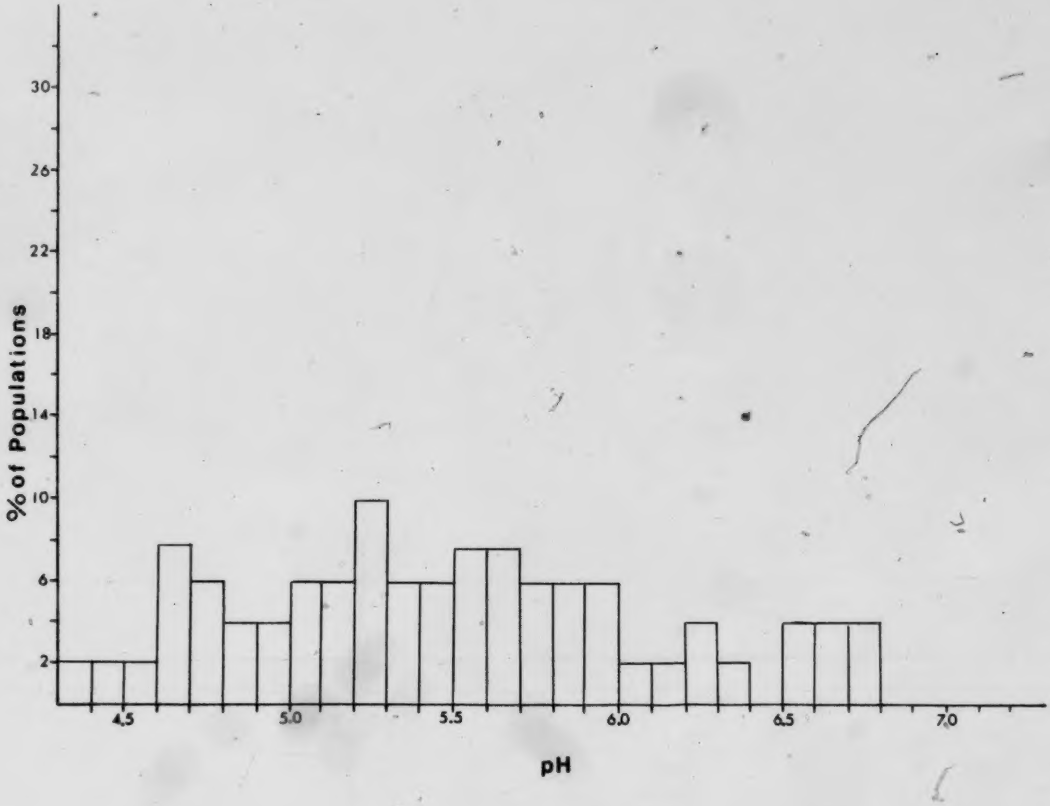

30
26
22
18
14
10
6
2
% of Populations
4.5
5.0
5.5
6.0
6.5
7.0
pH

FIGURE 25. *Pohlia annotina* (Hedw.) Lindb., resource utilization along organic matter and pH gradients
outer shaded = 90% of populations
middle striped = 50% of populations
inner black = 20% of populations.

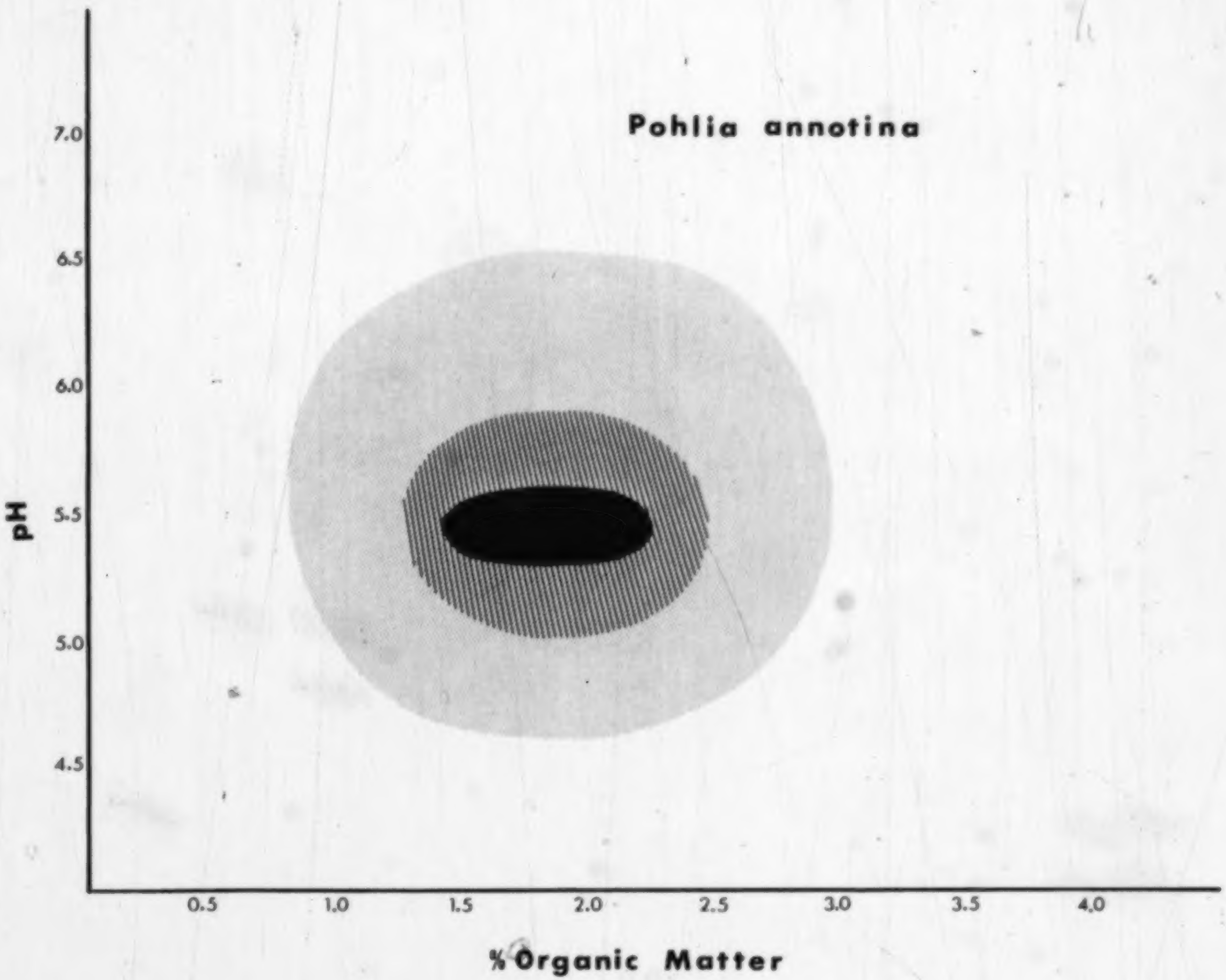
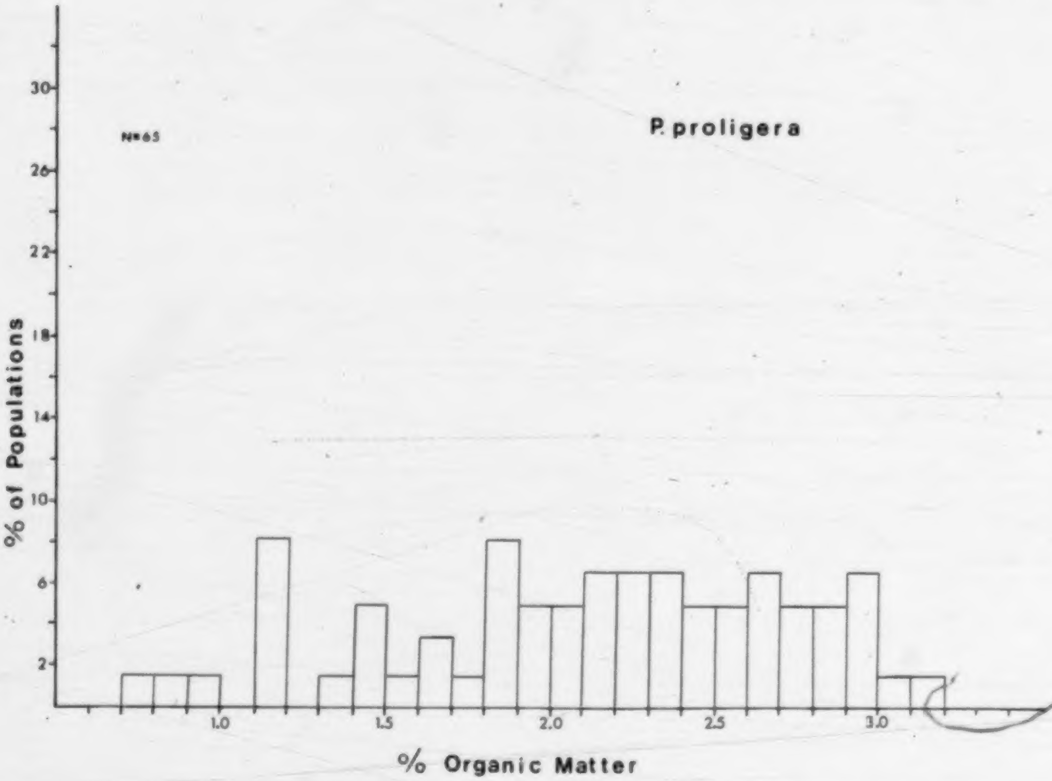

Pohlia annotina
pH
7.0
6.5
6.0
5.5
5.0
4.5
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
% Organic Matter

FIGURE 26. *Pohlia proligera* (Lindb. *ex* Breidl.) Lindb. *ex* Arn., histograms of resource utilization along organic matter and pH gradients.


P. proligera
N=65
% of Populations
30
26
22
18
14
10
6
2
1.0
1.5
2.0
2.5
3.0
% Organic Matter

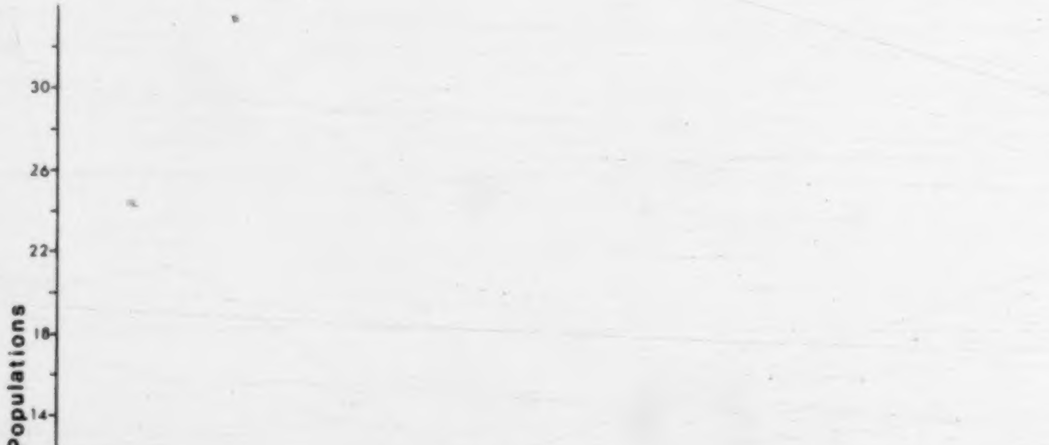

% of Populations
30
26
22
18
14
10
6
2
4.5
5.0
5.5
6.0
6.5
7.0
pH

FIGURE 27. *Pohlia proligera* (Lindb. *ex* Breidl.) Lindb. *ex* Arn., resource utilization along organic matter and pH gradients outer shaded = 90% of populations middle striped = 50% of populations inner black = 20% of populations.

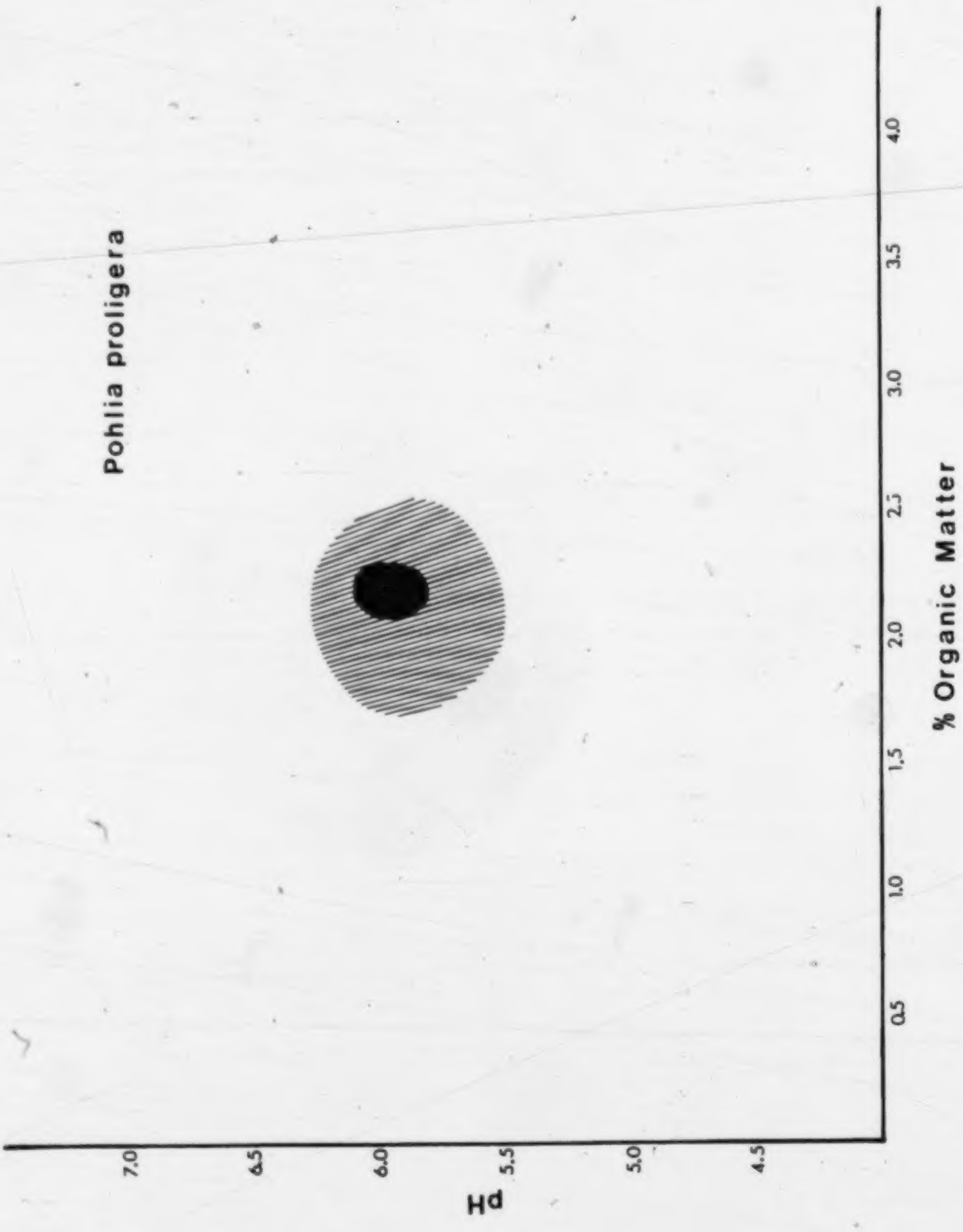
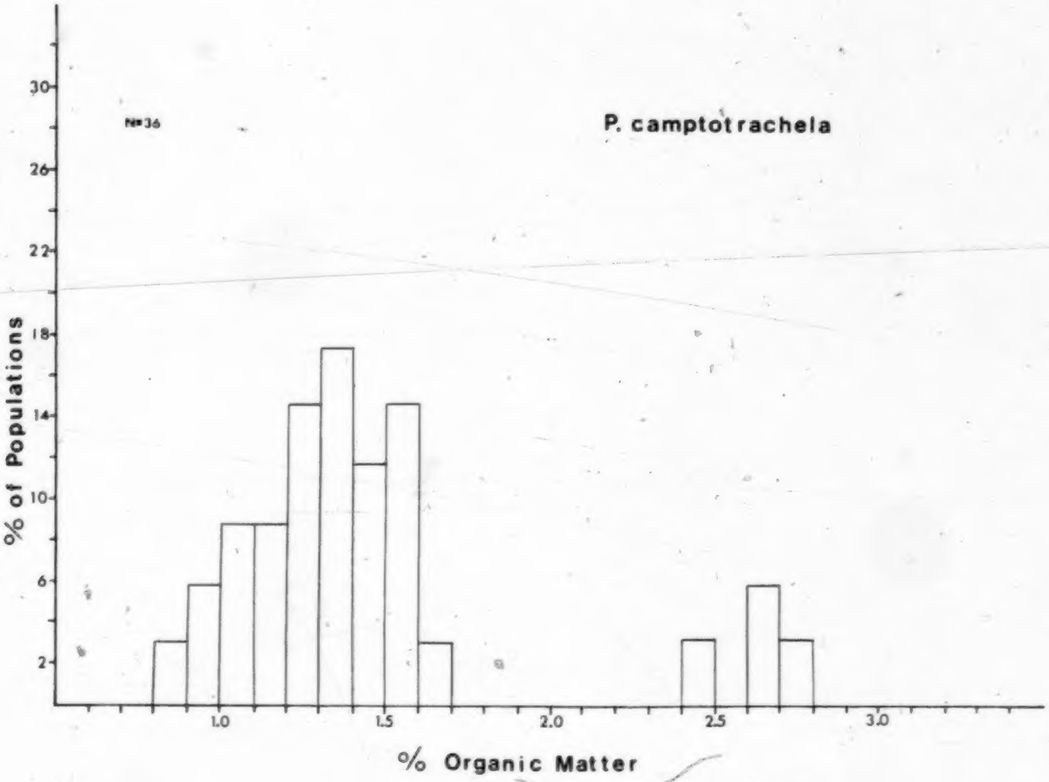

Pohlia proligera
% Organic Matter
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
pH
4.5
5.0
5.5
6.0
6.5
7.0

FIGURE 28. *Pohlia camptotrachela* (Ren. & Card.) Broth., histograms of resource utilization along organic matter and pH gradients.


N=36
P. camptotrachela
% of Populations
30
26
22
18
14
10
6
2
1.0
1.5
2.0
2.5
3.0
% Organic Matter

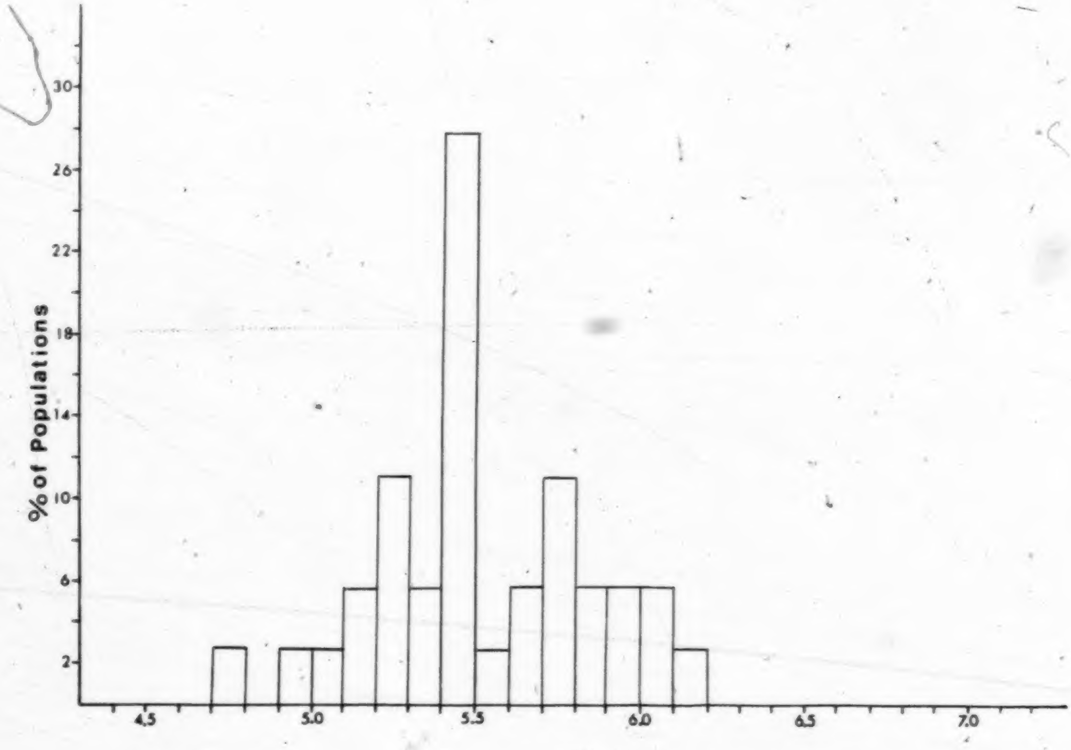
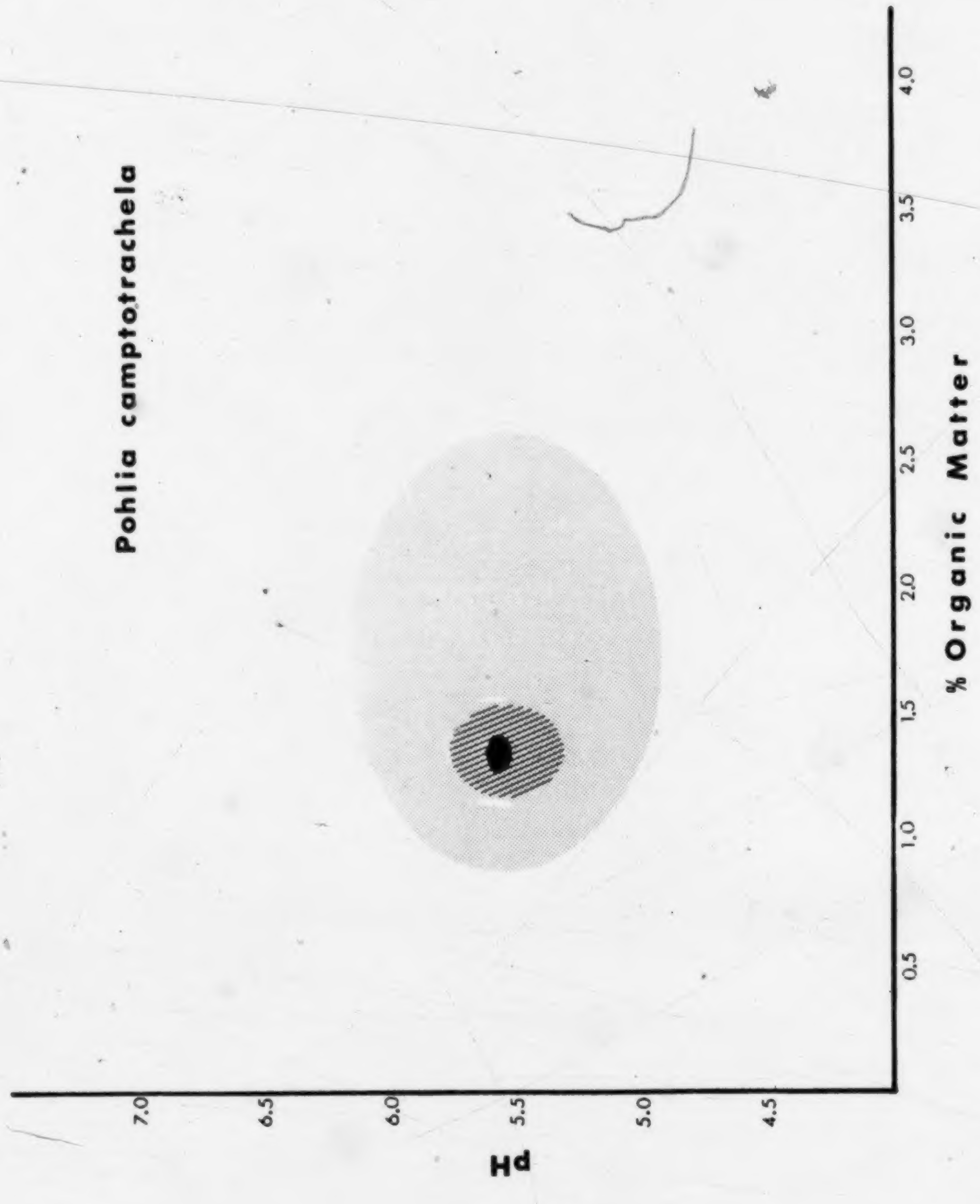
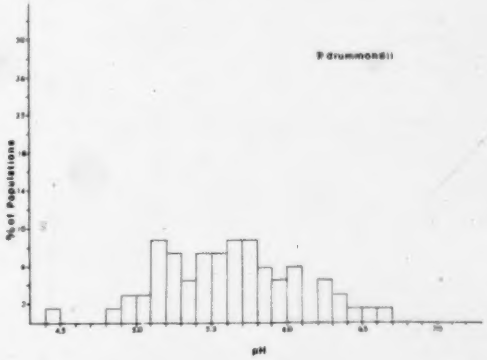

% of Populations
30
26
22
18
14
10
6
2
4.5
5.0
5.5
6.0
6.5
7.0
pH

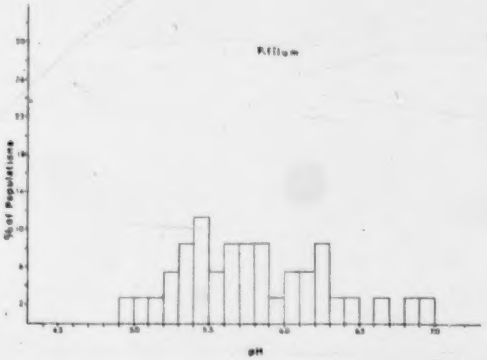
FIGURE 29. *Pohlia camptotrachela* (Ren. & Card.) Broth. resource utilization along organic matter and pH gradients
outer shaded = 90% of populations
middle striped = 50% of populations
inner black = 20% of populations.

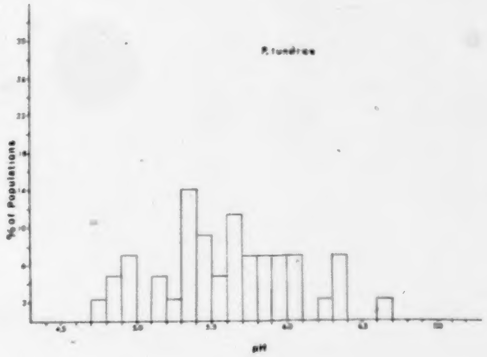


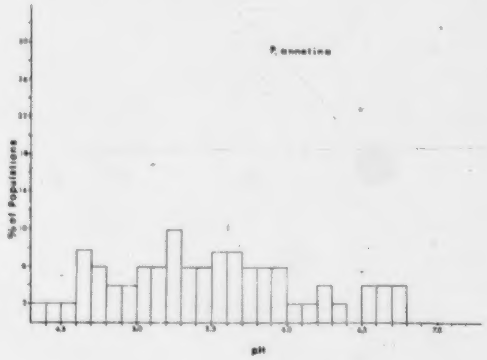
Pohlia camptotrachela

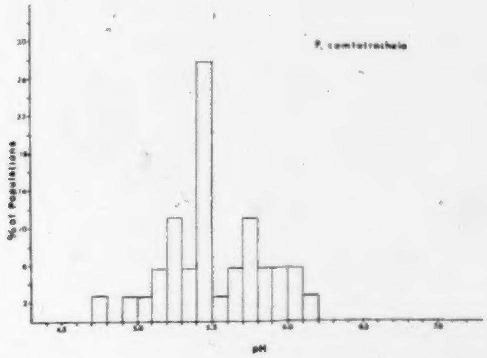
FIGURE 30. Comparison of resource utilization of propaguliferous species along the pH gradient.

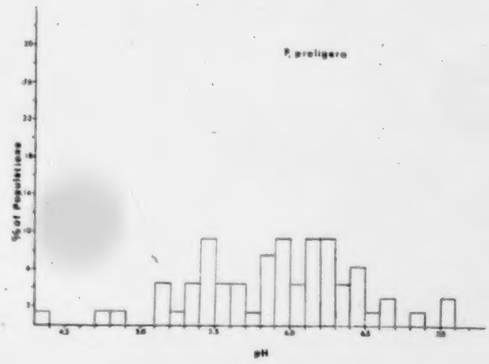

P. drummondii
% of Populations
2
6
10
14
18
22
26
30
4.5
5.0
5.5
6.0
6.5
7.0
pH


P. filum
% of Populations
2
6
10
14
18
22
26
30
4.5
5.0
5.5
6.0
6.5
7.0
pH


P. tundrae
% of Populations
2
6
10
14
18
22
26
30
4.5
5.0
5.5
6.0
6.5
7.0
pH


P. annotina
% of Populations
2
6
10
14
18
22
26
30
4.5
5.0
5.5
6.0
6.5
7.0
pH


P. camtotrachela
% of Populations
2
6
10
14
18
22
26
30
4.5
5.0
5.5
6.0
6.5
7.0
pH


P. proligera
% of Populations
2
6
10
14
18
22
26
30
4.5
5.0
5.5
6.0
6.5
7.0
pH

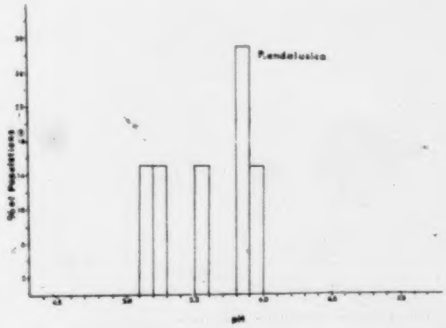
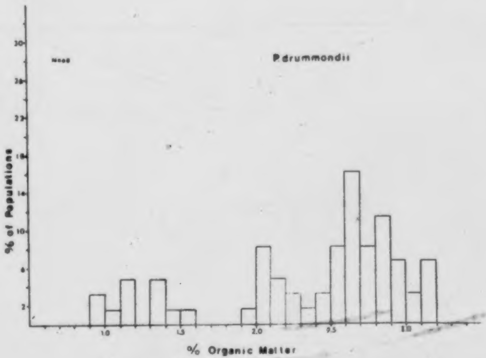
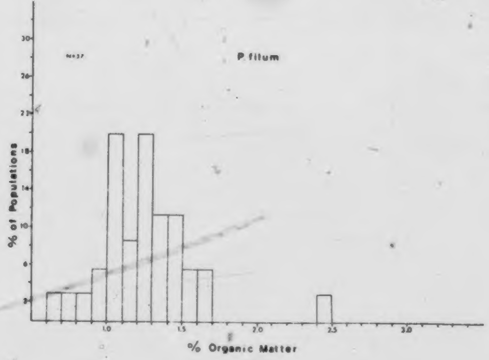
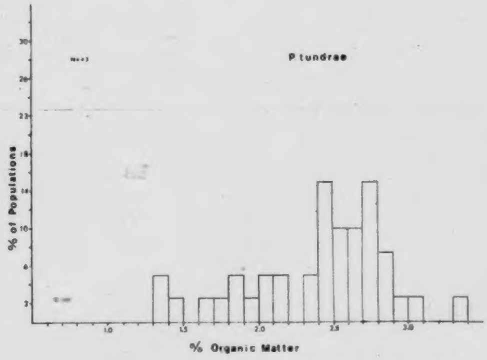
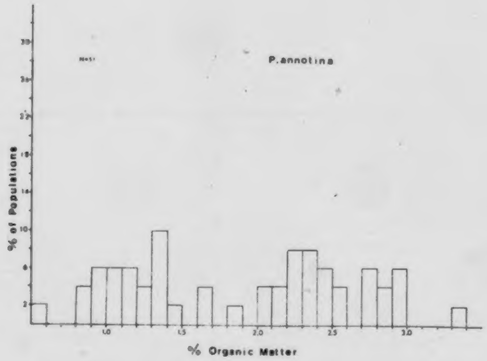

P. andalusica
% of Populations
2
6
10
14
18
22
26
30
4.5
5.0
5.5
6.0
6.5
7.0
pH

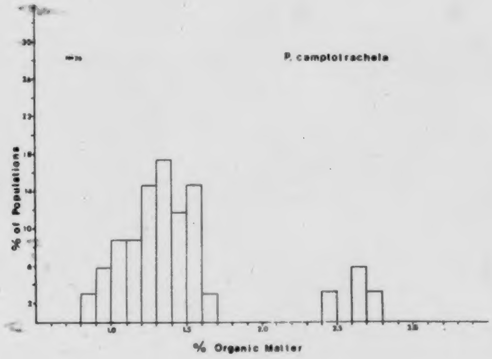
FIGURE 31. Comparison of resource utilization of propaguliferous species along the organic matter gradient.

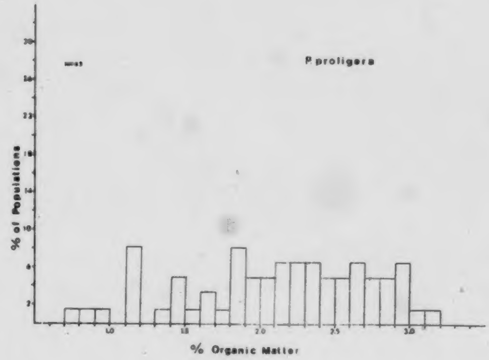

P.drummondii
% of Populations
30
26
22
18
14
10
6
2
1.0
1.5
2.0
2.5
3.0
% Organic Matter


N=37
P.filum
% of Populations
30
26
22
18
14
10
6
2
1.0
1.5
2.0
2.5
3.0
% Organic Matter


P.tundrae
% of Populations
30
26
22
18
14
10
6
2
1.0
1.5
2.0
2.5
3.0
% Organic Matter


P.annotina
% of Populations
30
26
22
18
14
10
6
2
1.0
1.5
2.0
2.5
3.0
% Organic Matter


P. camptotrachela
% of Populations
30
26
22
18
14
10
6
2
1.0
1.5
2.0
2.5
3.0
% Organic Matter


P.proligera
% of Populations
30
26
22
18
14
10
6
2
1.0
1.5
2.0
2.5
3.0
% Organic Matter

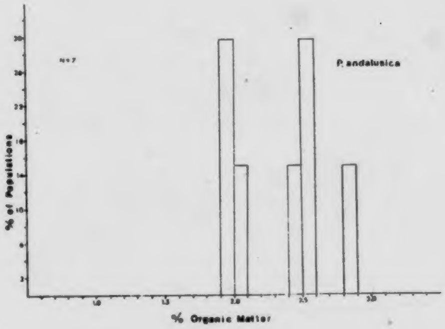
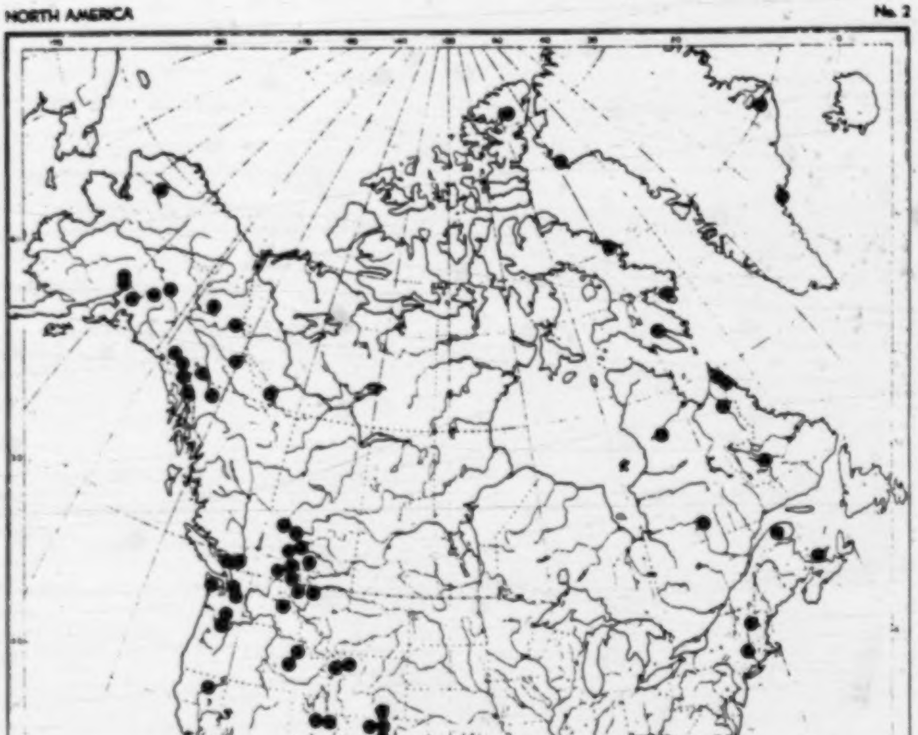

N=7
P.andalusica
% of Populations
30
26
22
18
14
10
6
2
1.0
1.5
2.0
2.5
3.0
% Organic Matter

FIGURE 32. *Pohlia drummondii* (C. Müll.) Andr., geographic distribution.


NORTH AMERICA
No. 2
SCALE
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
GOODE BASE MAP SERIES

P.drummondii

FIGURE 33. *Pohlia drummondii* (C. Müll.) Andr.
1-8 Stem leaves (x36)
9 Perichaetial leaf (x36)
10 Upper leaf cells (x390)
11 Exothecial cells (x390)
12 Costa, transverse section (x390)
13 Capsule, dry (x12)
14 Capsule, moist (x12)
15,16 Perigonial plants (x10).

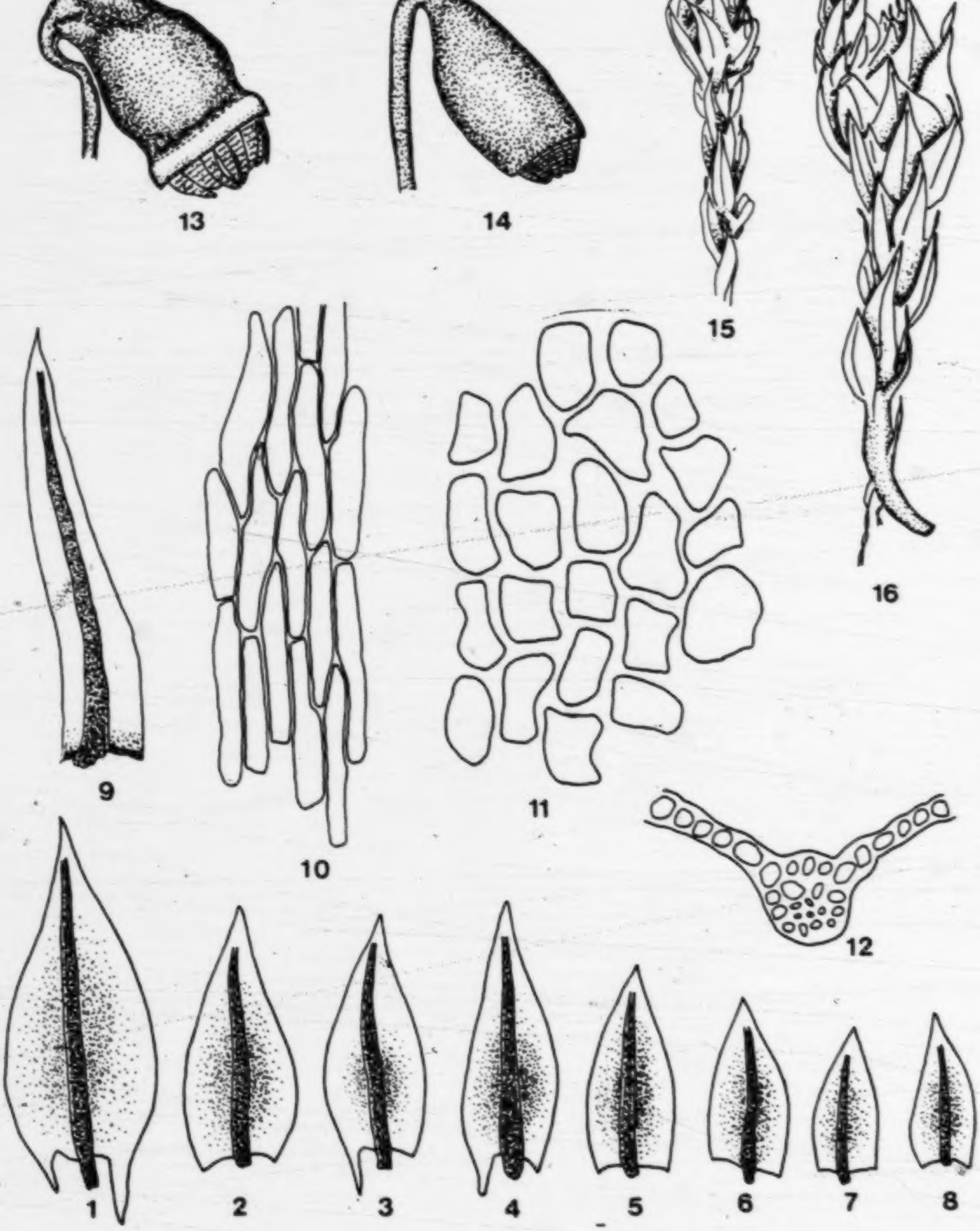


FIGURE 34. *Pohlia drummondii* (C. Müll.) Andr., propagula (x288).

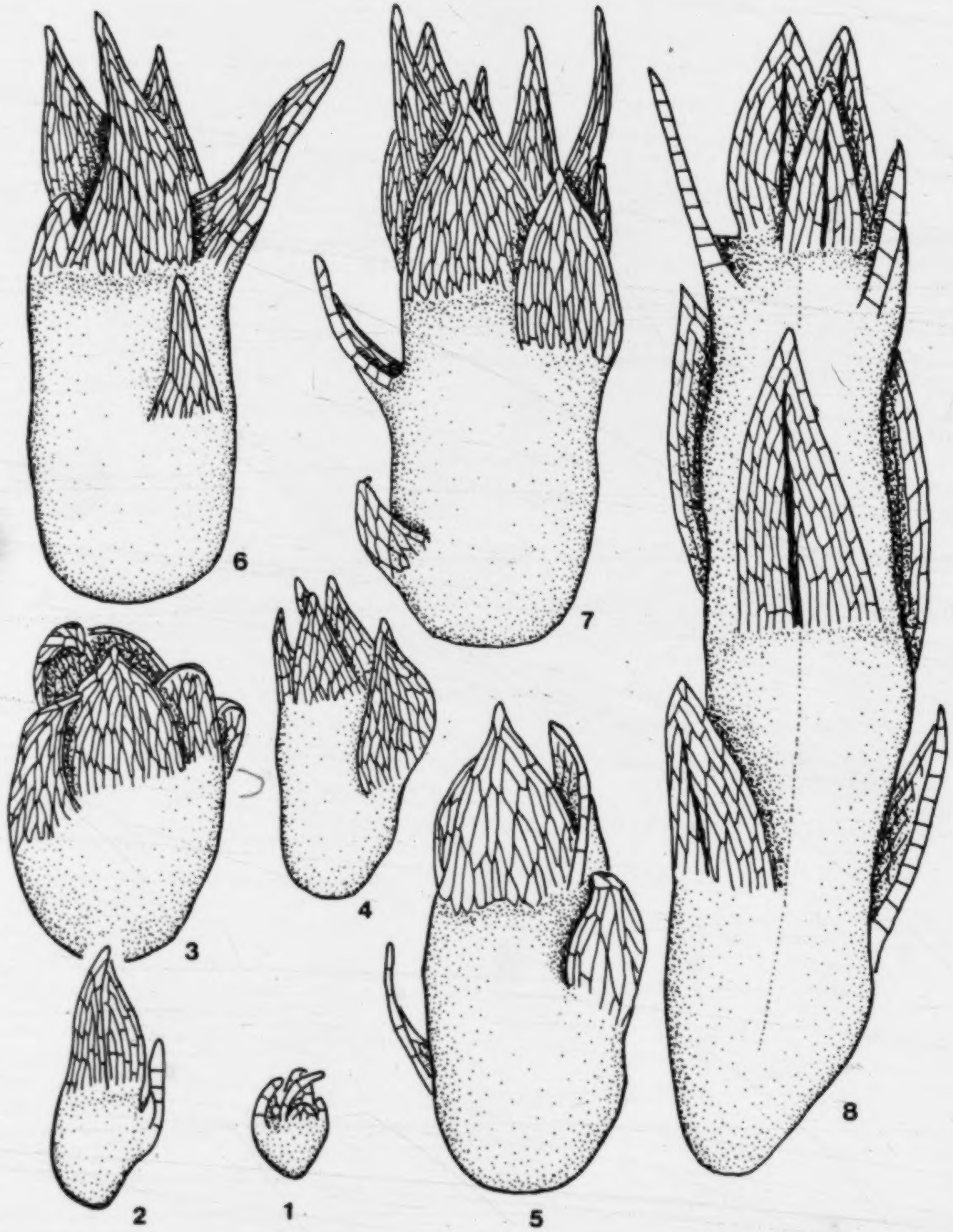


FIGURE 35. *Pohlia filum* (Schimper) Mårt., geographic distribution.

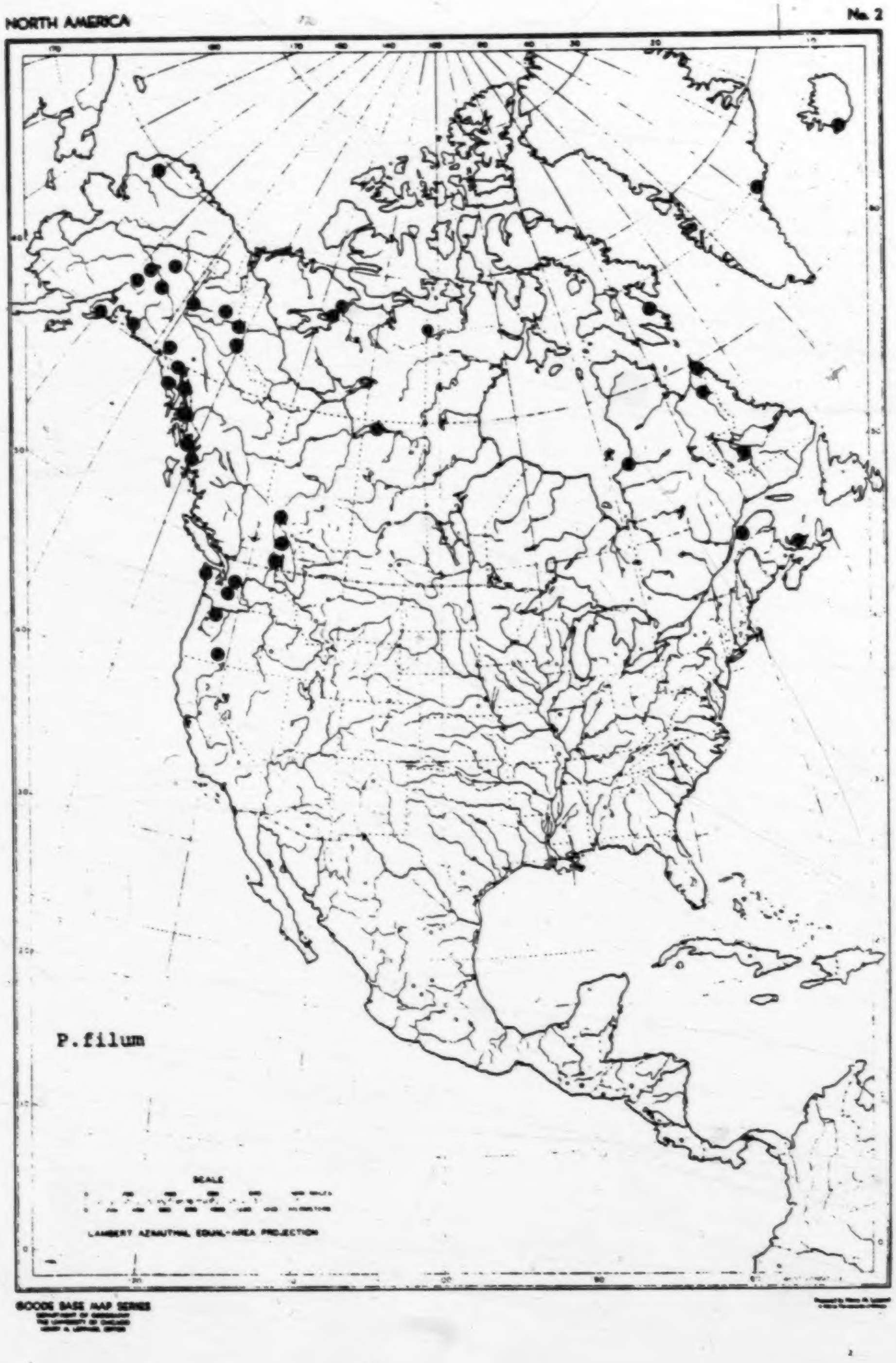

NORTH AMERICA
No. 2
P.filum
SCALE
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR

FIGURE 36. *Pohlia filum* (Schimper) Mårt.

1-10	Stem leaves (x36)
11	Perichaetial leaf (x36)
12	Upper leaf cells (x390)
13	Exothecial cells (x390)
14	Costa, transverse section (x390)
15	Capsule, dry (x12)
16	Capsule, moist (x12)
17-19	Perigonial plants (x12).

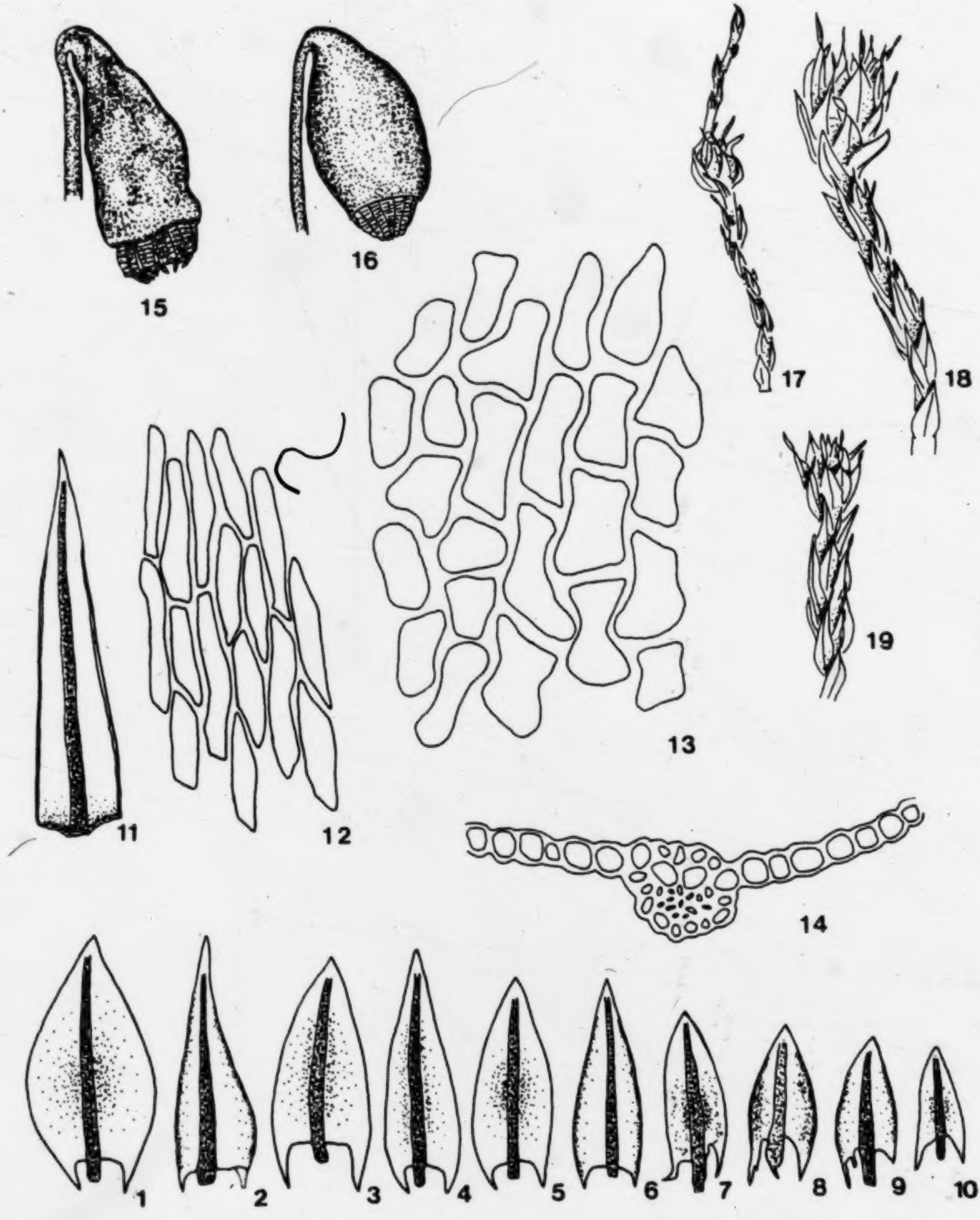


FIGURE 37. *Pohlia filum* (Schimper) Mårt.
1-6 Propagula (x288)
7 Sterile shoot with propagula (x10).

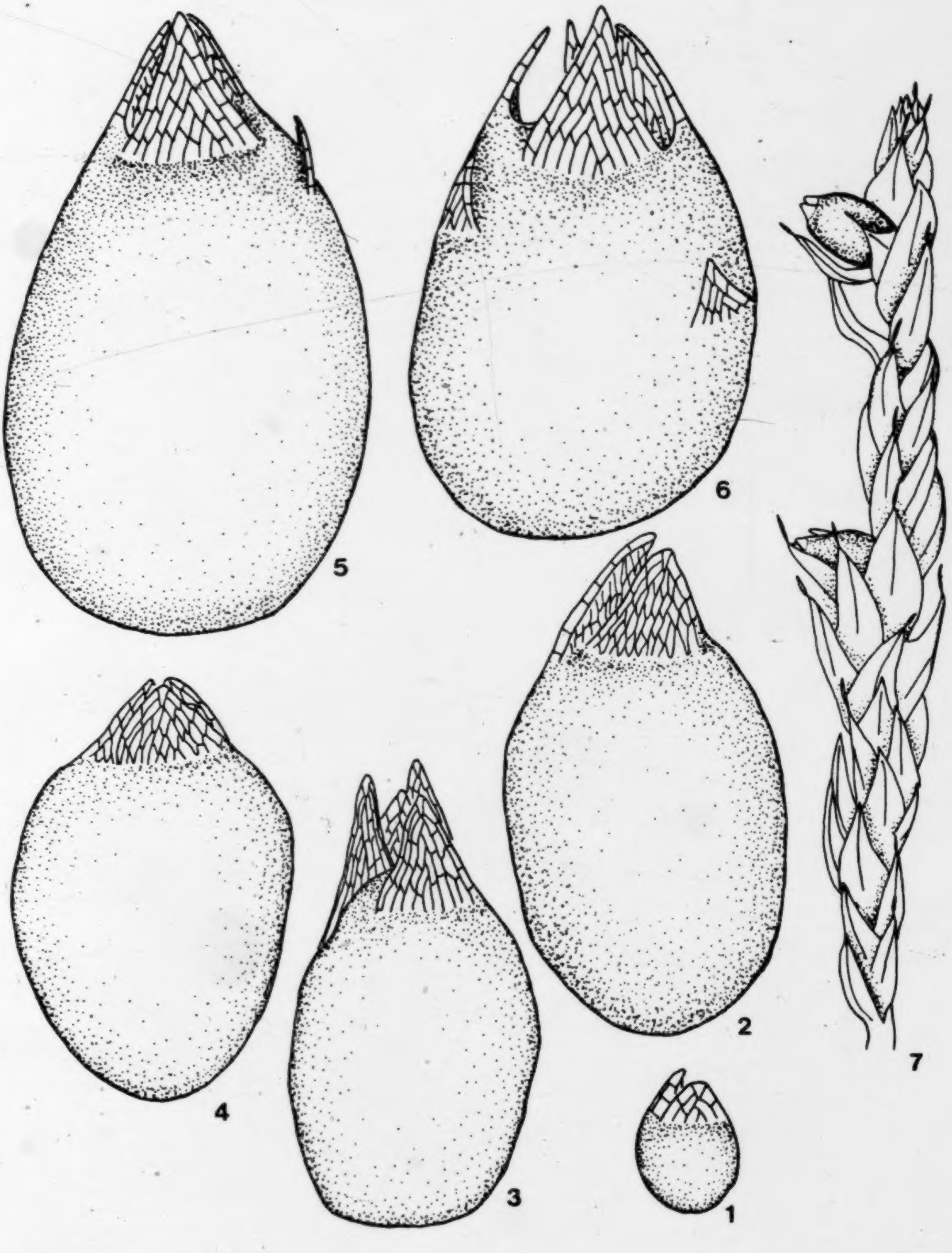


FIGURE 38. *Pohlia andalusica* (Höhnel) Broth., geographic distribution.

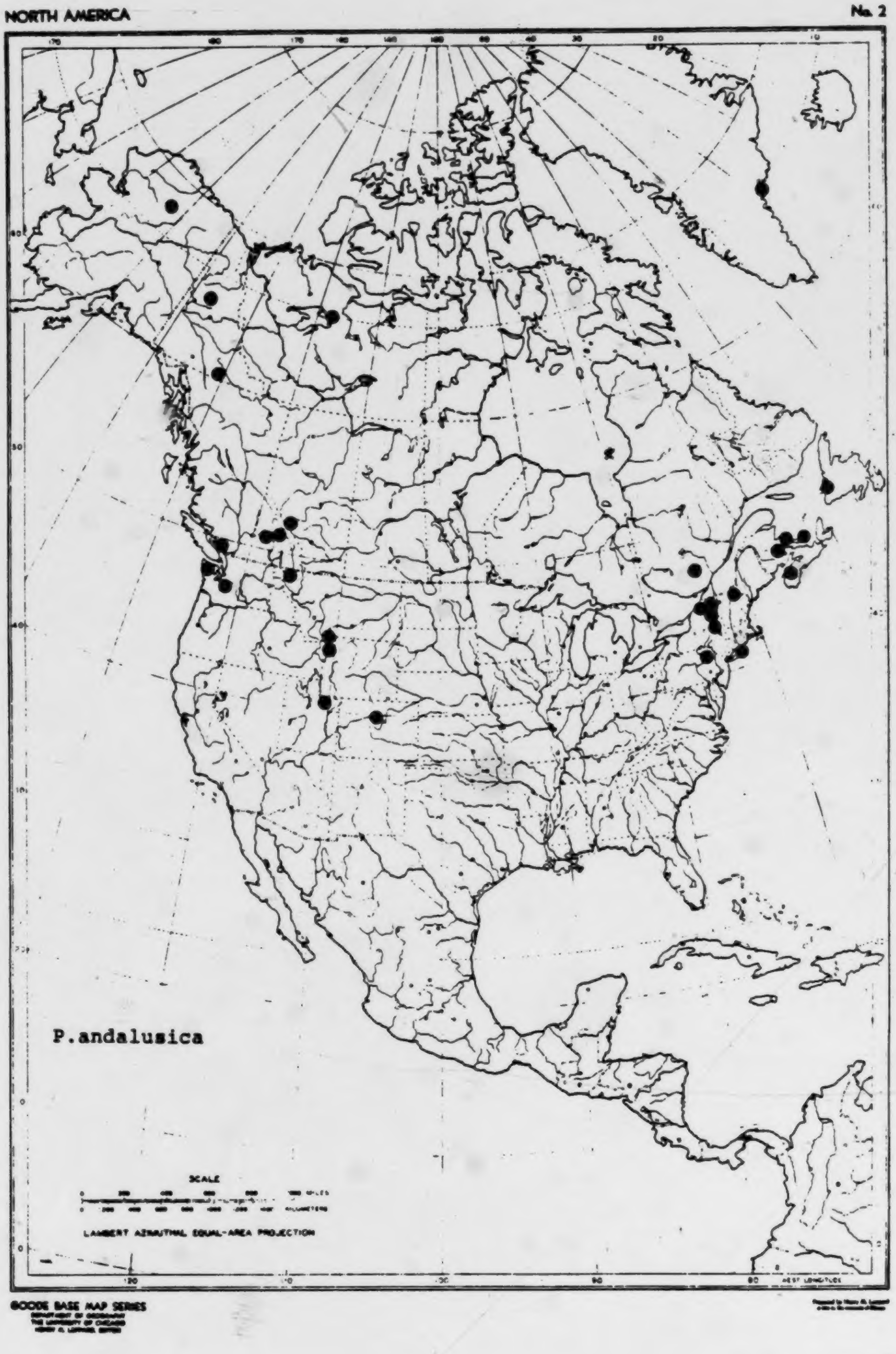

NORTH AMERICA
No. 2
P.andalusica
SCALE
MILES
KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
120
110
100
90
80
WEST LONGITUDE
GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR

FIGURE 39. *Pohlia andalusica* (Höhnel) Broth.

1-10	Stem leaves from just below apex (x36)
11	Perichaetial leaf (x36)
12	Upper leaf cells (x390)
13	Costa, transverse section (x390)
14	Exothecial cells (x390)
15	Capsule, dry (x12)
16	Capsule, moist (x12)
17,18	Perigonial plants (x10).

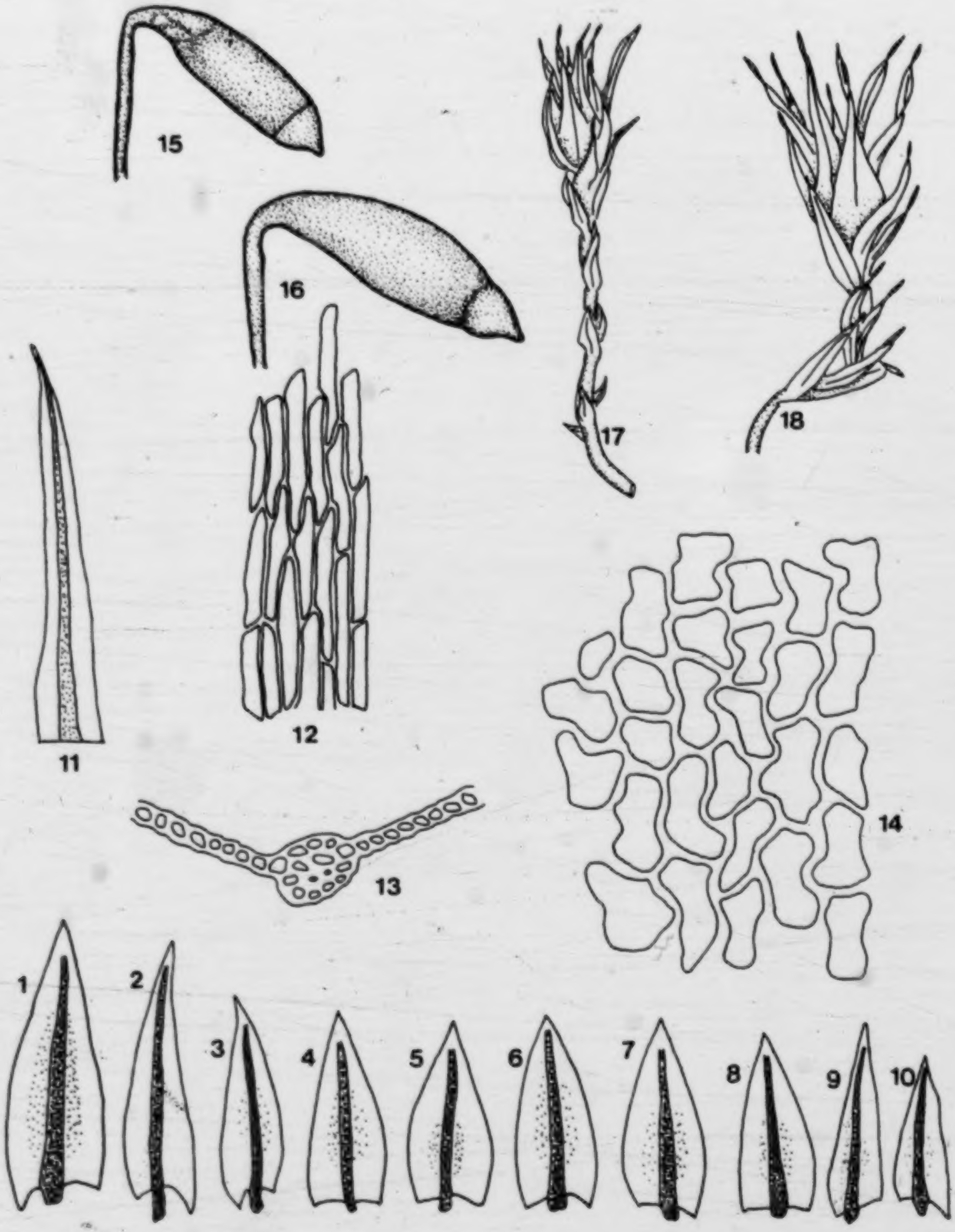


FIGURE 40. *Pohlia andalusica* (Höhnel) Broth., propagula (x288).

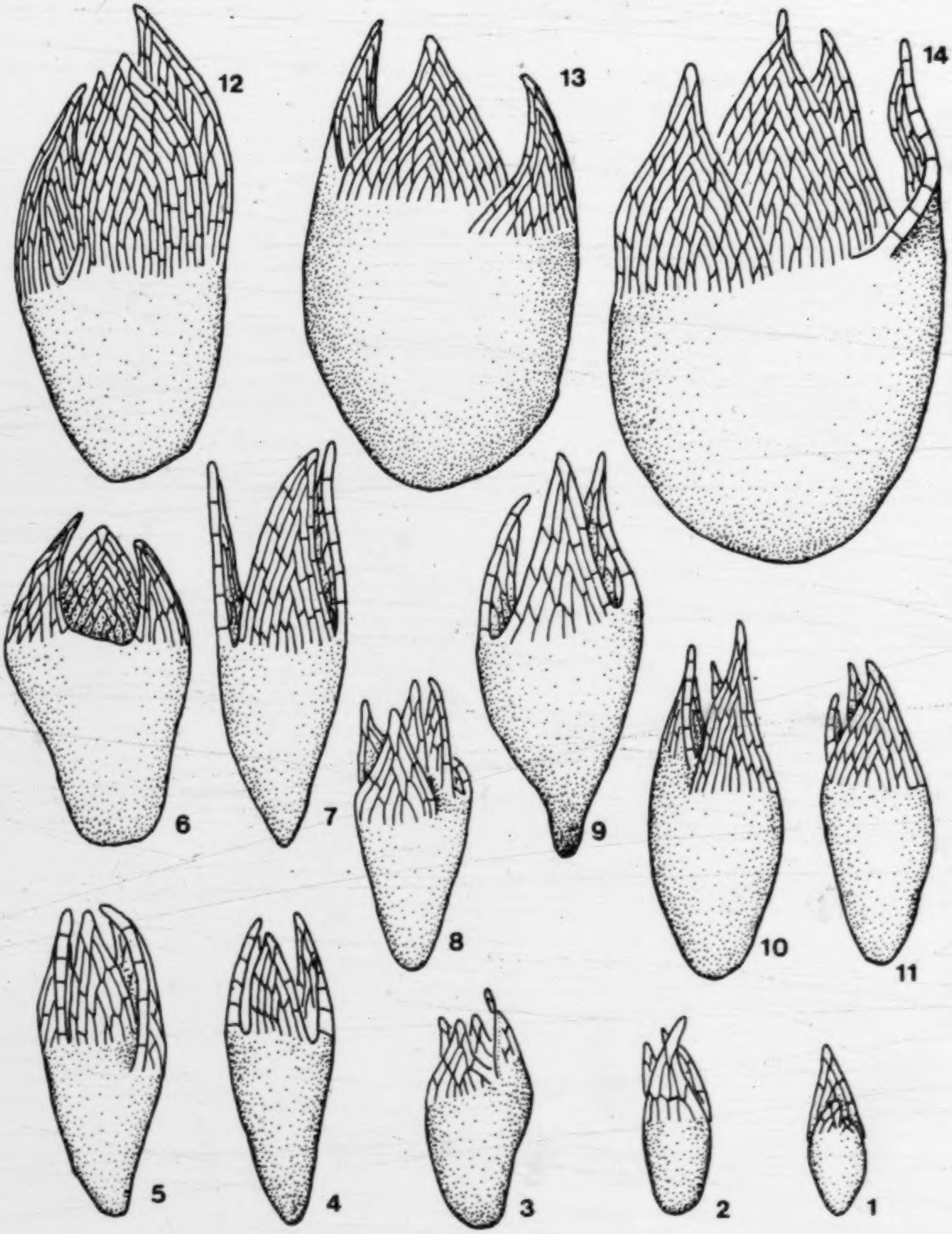


FIGURE 41. *Pohlia tundrae* J. Shaw, geographic distribution.

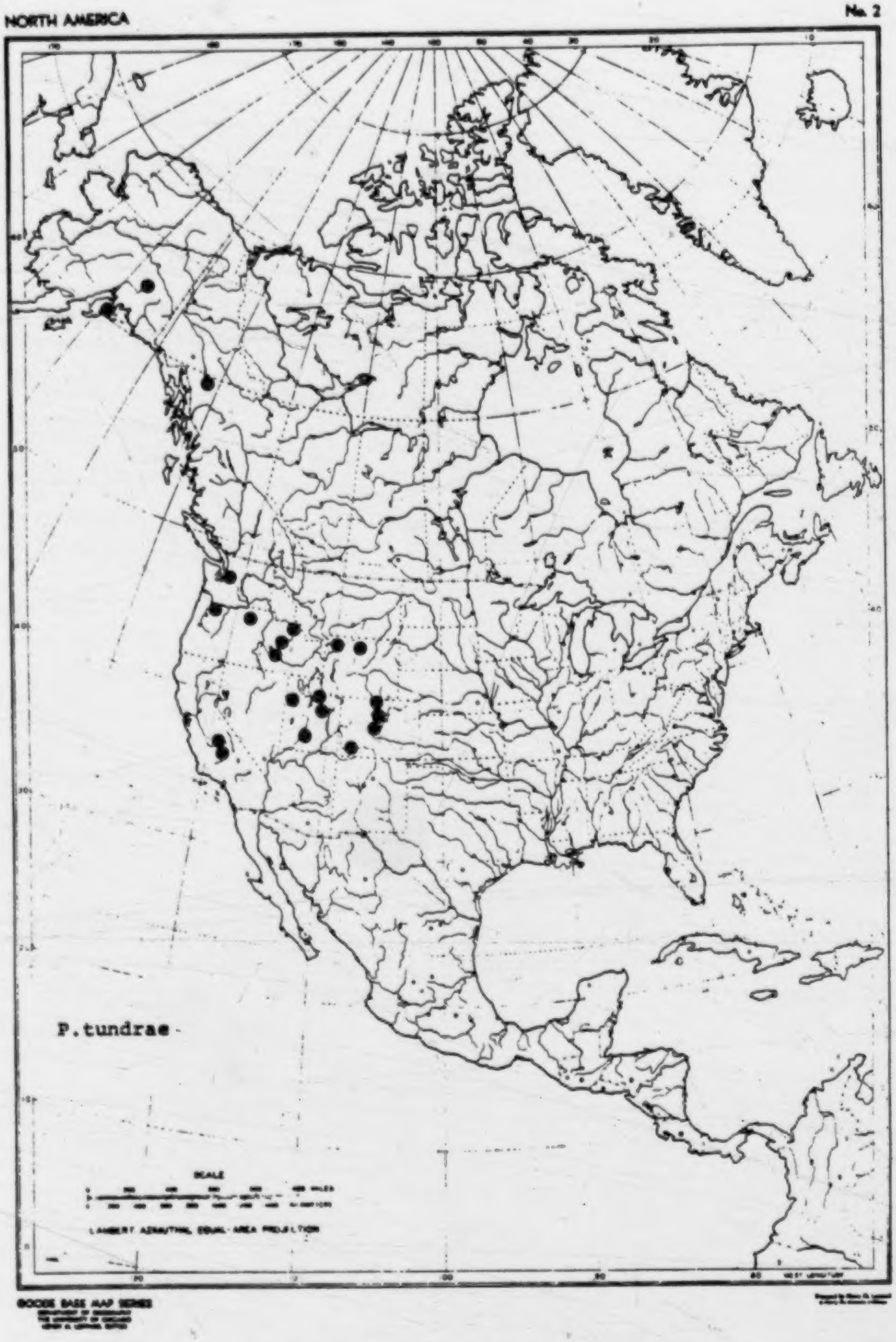

NORTH AMERICA
No. 2
P.tundrae
SCALE
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
GOODE BASE MAP SERIES

FIGURE 42. *Pohlia tundrae* J. Shaw
1-10 Stem leaves from just below stem apex (x36)
11,12 Perichaetial leaves (x36)
13 Upper leaf cells (x390)
14 Exothecial cells (x390)
15 Costa, transverse section (x390)
16 Capsule, moist (x12)
17 Capsule, dry (x12)
18 Perigonial plant, rare basal branching (x10)
19 Perigonial plant, typical subfloral branching (x10).

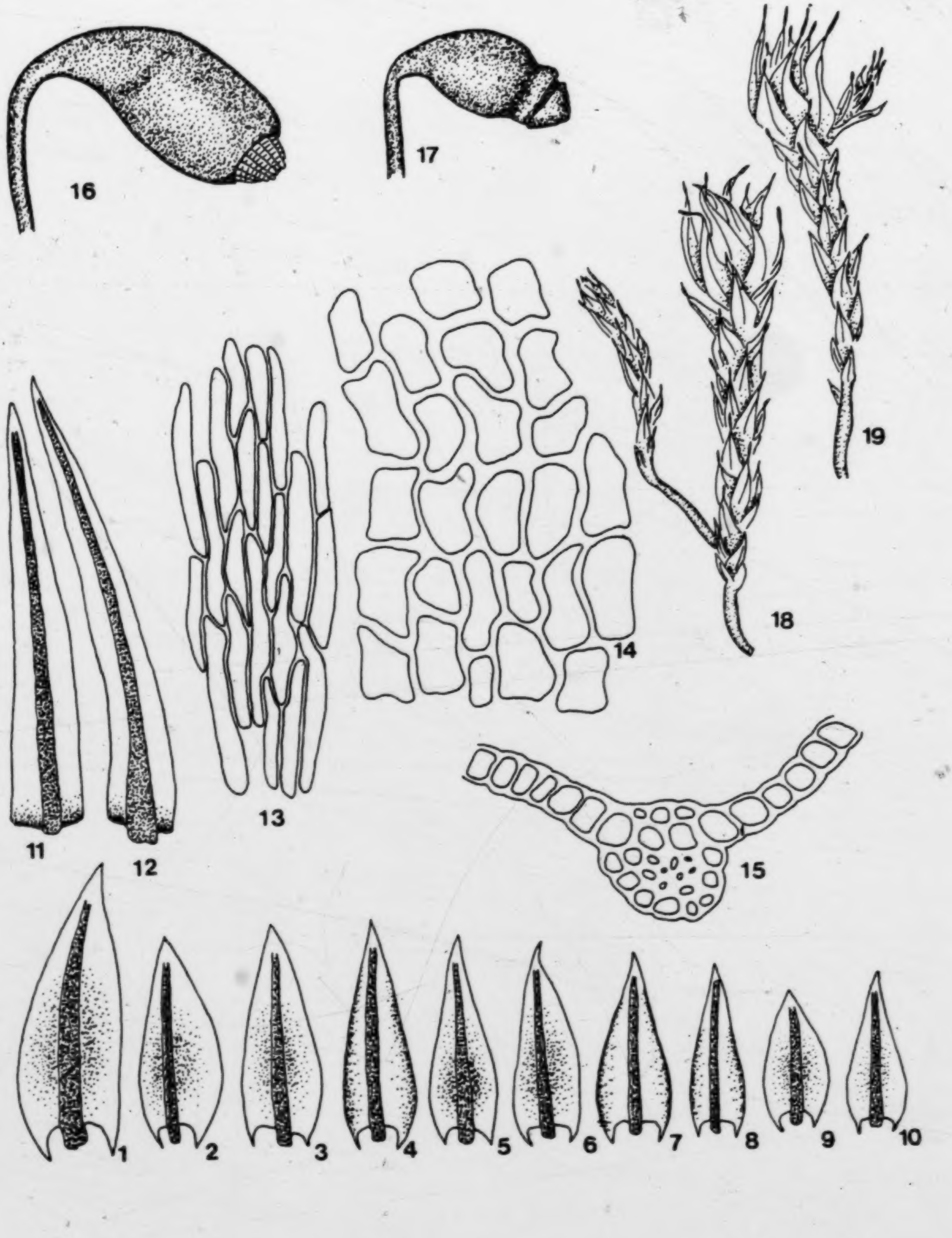


FIGURE 43. *Pohlia tundrae* J. Shaw, propagula (x288).

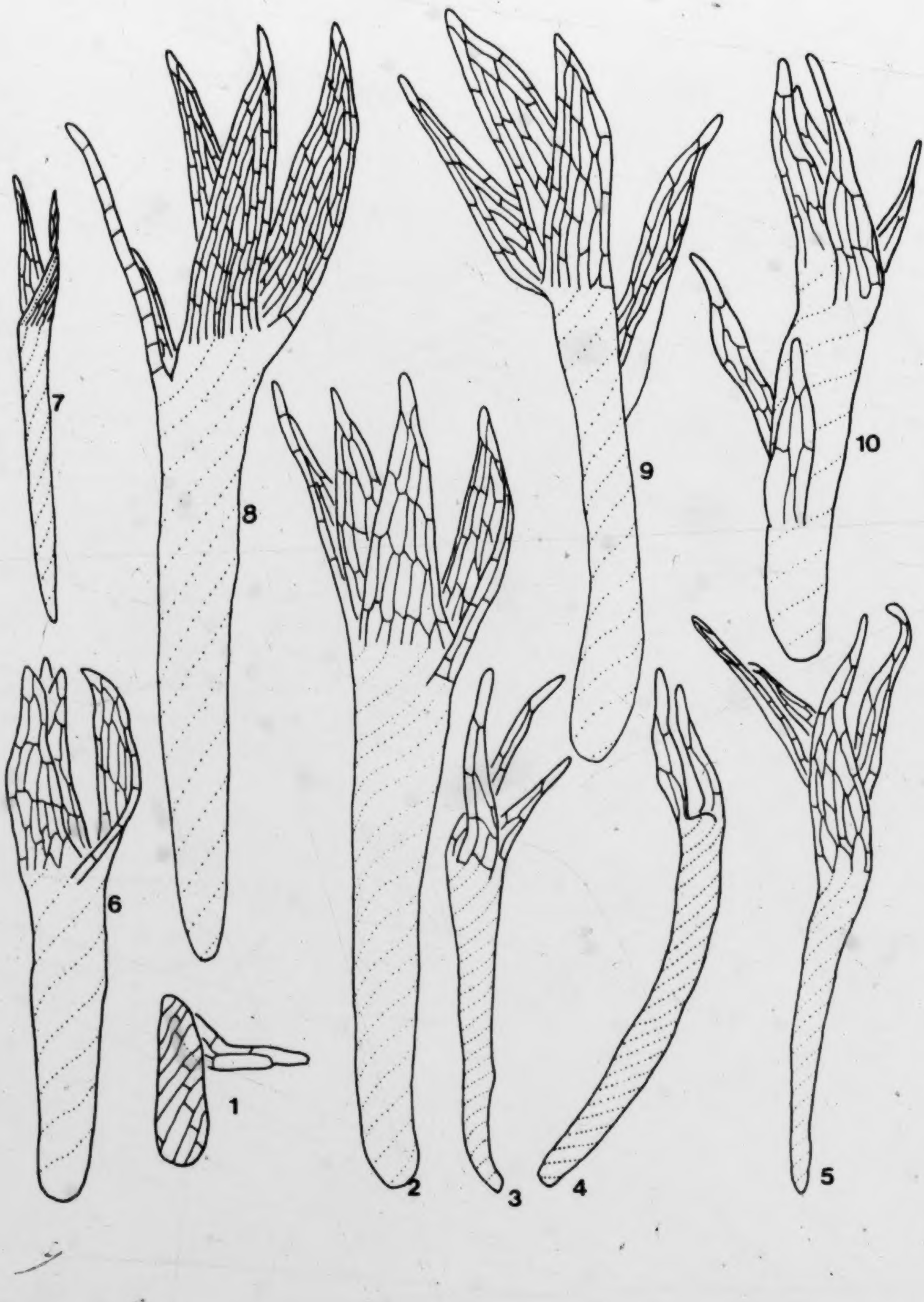


FIGURE 44. Scatter diagram comparing *Pohlia annotina* (Hedw.) Lindb. and *P. tundrae* J. Shaw with respect to propagulum body length and leaf primordium length. Integers represent the number of cells constituting the base of leaf primordia, and are derived from the mean value for 10 propagula in a population, rounded to the nearest whole number
Shaded = plants with dull leaves (*P. annotina*)
Unshaded = plants with glossy leaves (*P. tundrae*)

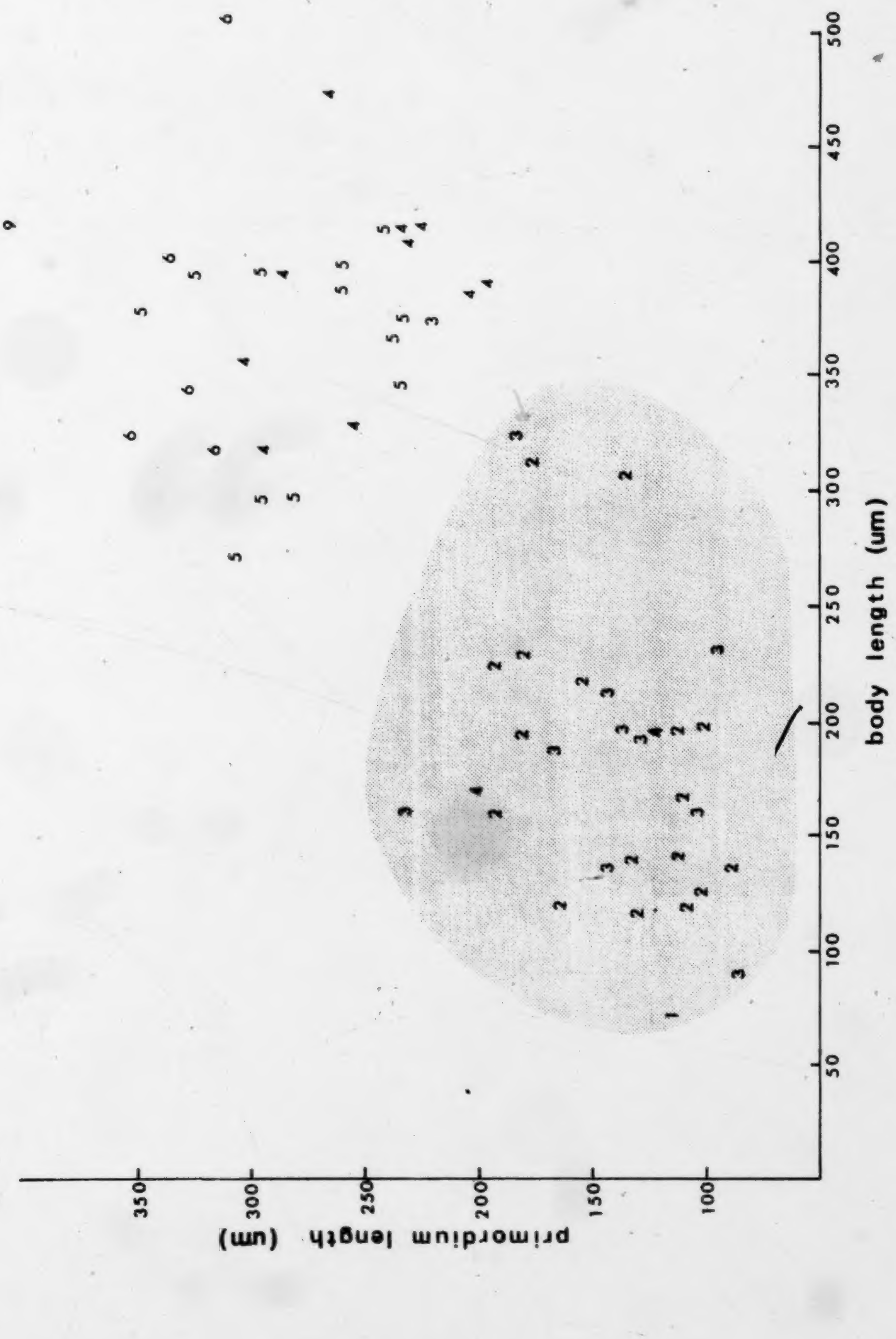
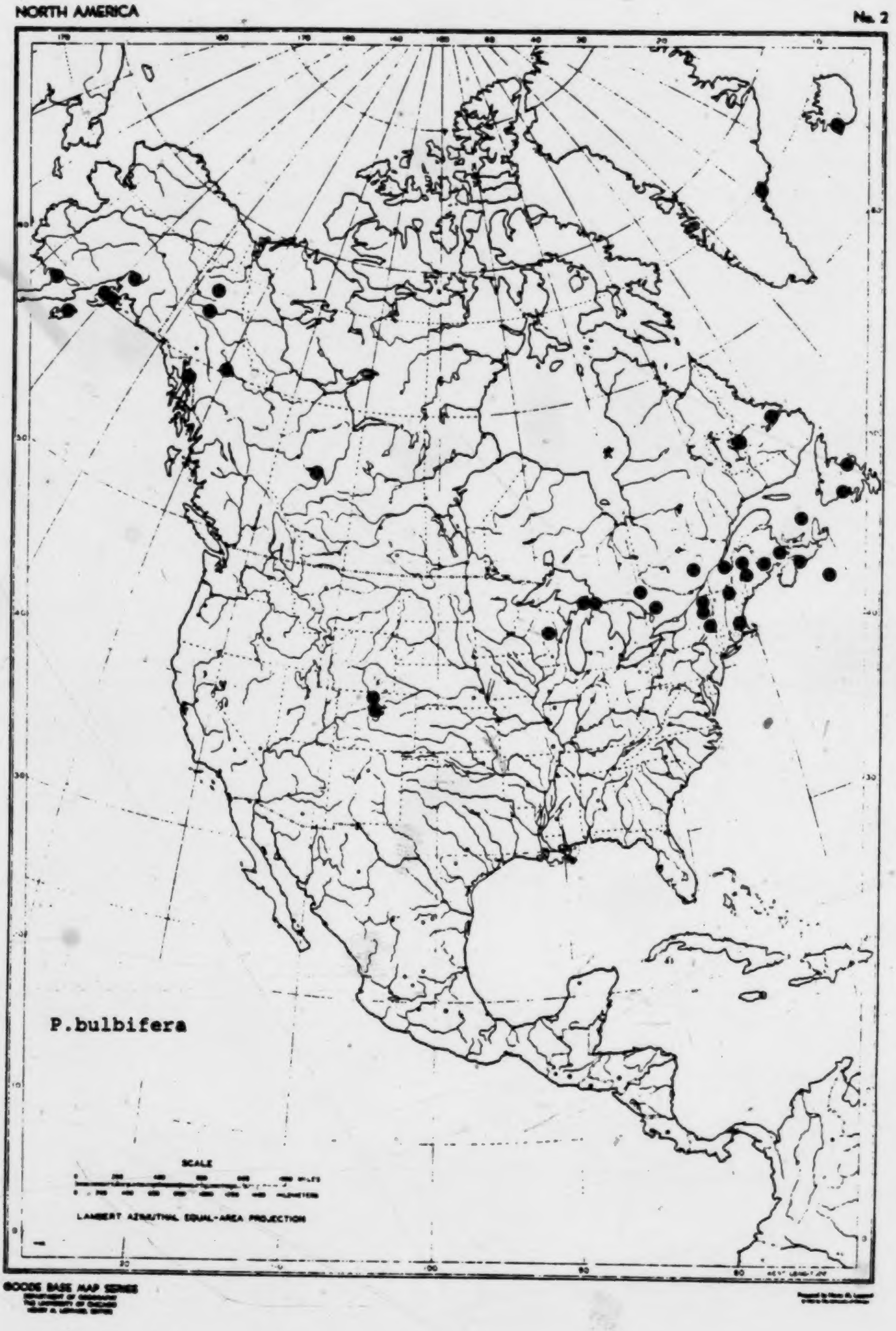

primordium length (um)
350
300
250
200
150
100
body length (um)
50
100
150
200
250
300
350
400
450
500

FIGURE 45. *Pohlia bulbifera* (Warnst.) Warnst., geographic distribution.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GOODE BASE MAP SERIES

P.bulbifera

FIGURE 46. *Pohlia bulbifera* (Warnst.) Warnst.
1-8 Stem leaves from just below apex (x36)
9 Perichaetial leaf (x36)
10 Exothecial cells (x300) (x390)
11 Upper leaf cells (x300) (x390)
12 Costa, transverse section (x390)
13 Capsule, dry (x12)
14 Capsule, moist (x12)
15,16 Perigonial plants (x10).

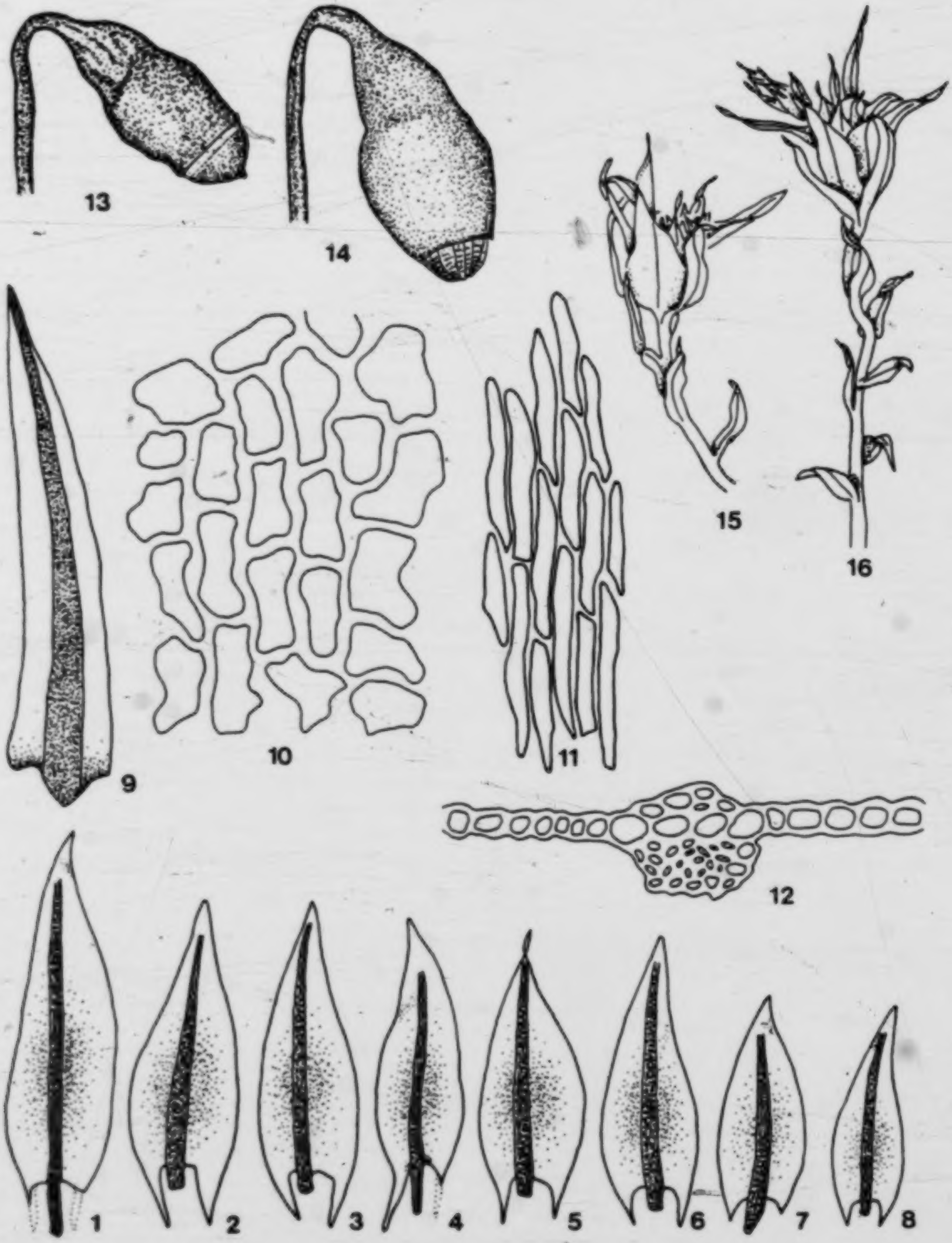
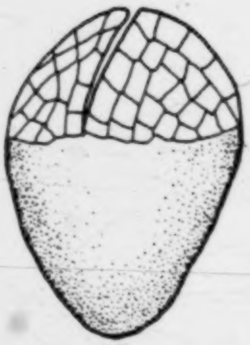


FIGURE 47. *Pohlia bulbifera* (Warnst.) Warnst., propagula (x288).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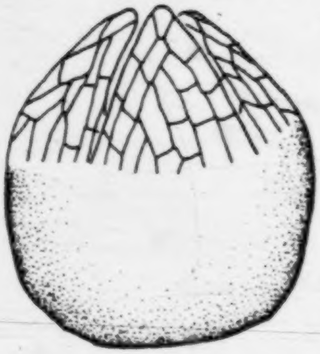
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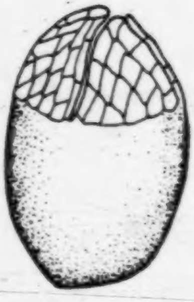
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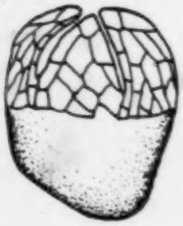
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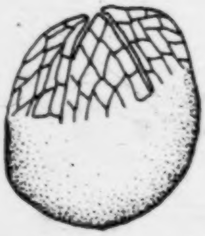
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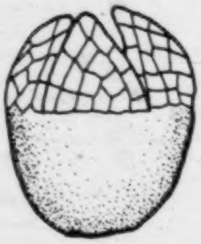
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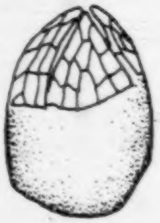
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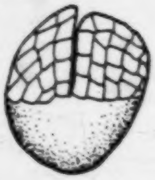
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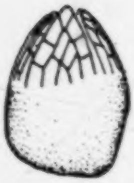
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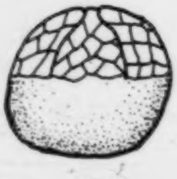
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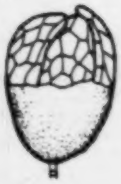
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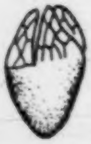
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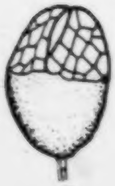
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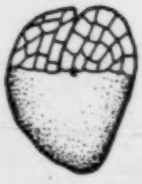
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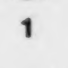
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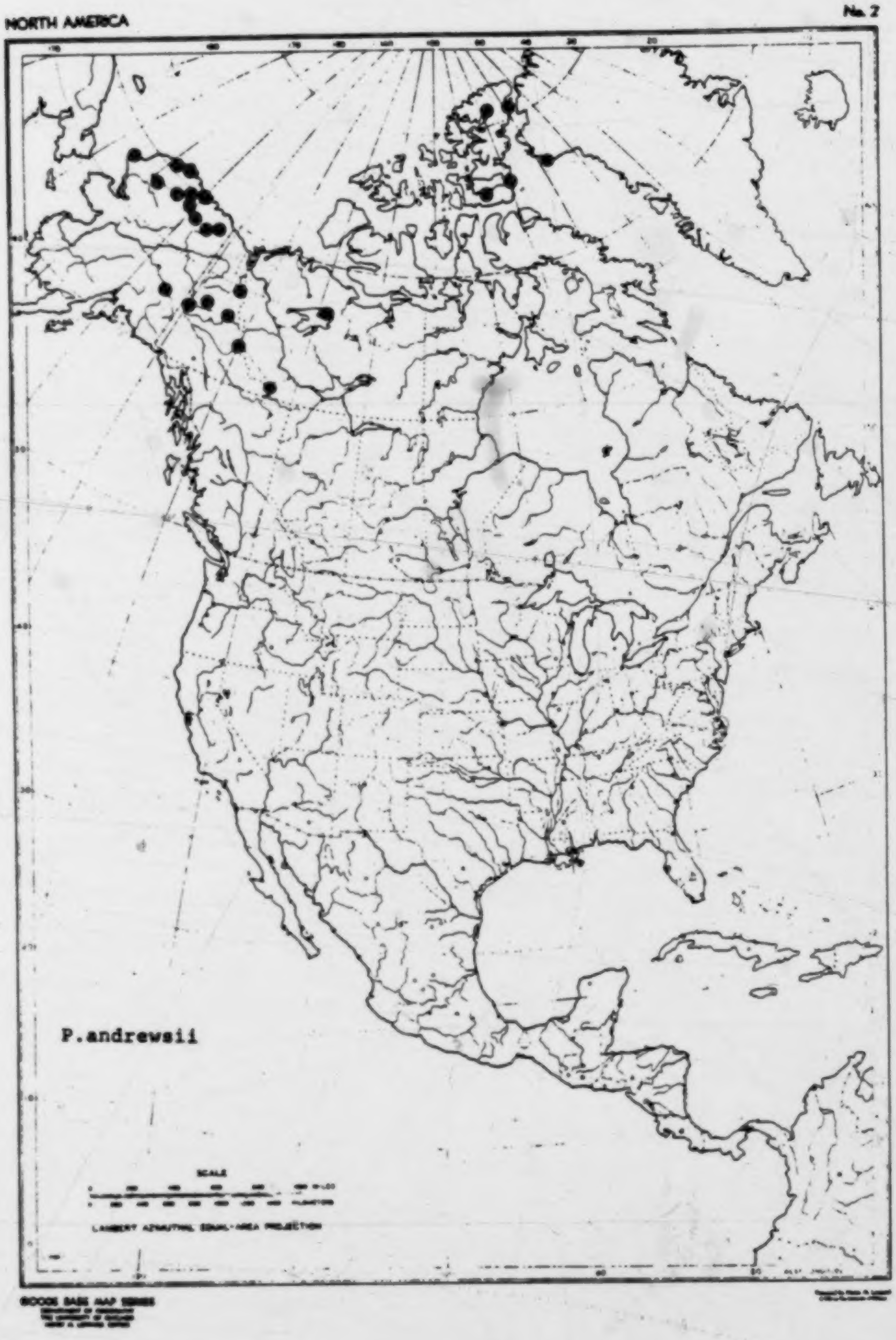
FIGURE 48. *Pohlia andrewsii* J. Shaw, geographic distribution.


NORTH AMERICA
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P.andrewsii
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GOODE BASE MAP SERIES

FIGURE 49. *Pohlia andrewsii* J. Shaw

1-8 Stem leaves from just below apex (x36)
9 Perichaetial leaf (x36)
10 Exothecial cells (x300) (x390)
11 Costa, transverse section (x390)
12 Upper leaf cells (x390)
13-15 Perigonial plants showing range of variation in outer bract length (x10)
16 Capsule, moist (x12)
17 Capsule, dry (x12)

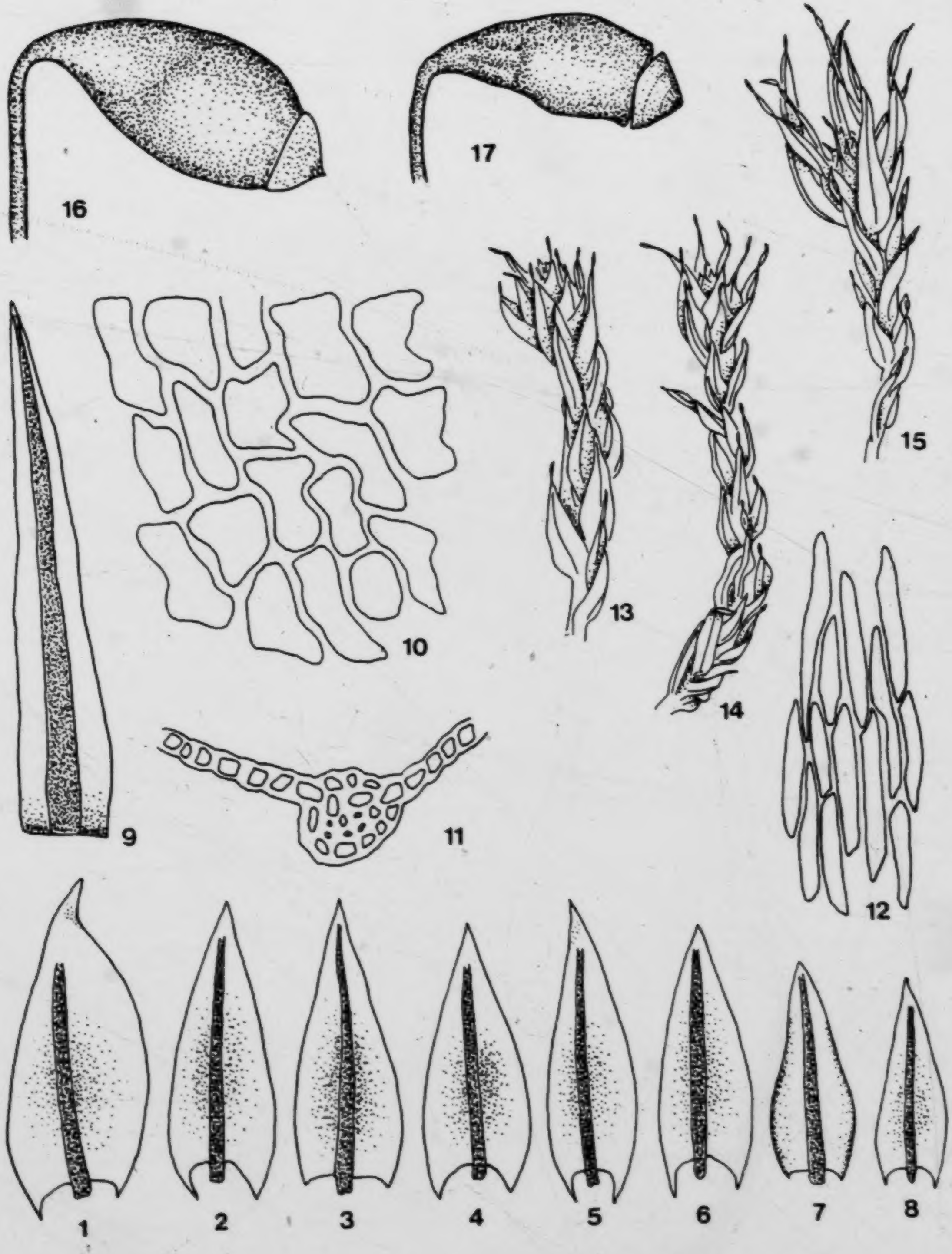
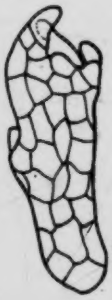


FIGURE 50. *Pohlia andrewsii* J. Shaw, propagula (x288).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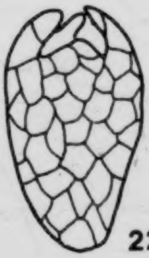
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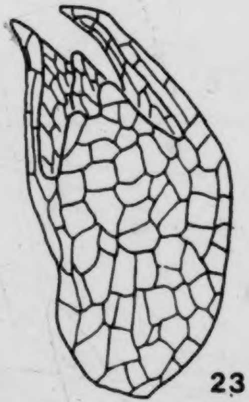
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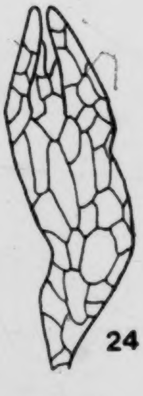
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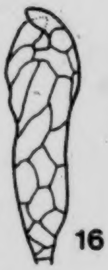
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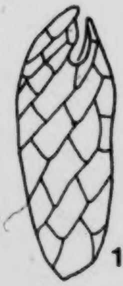
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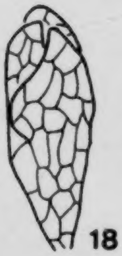
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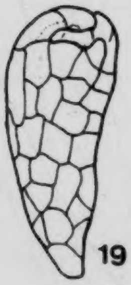
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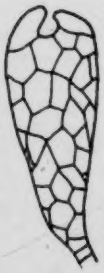
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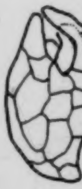
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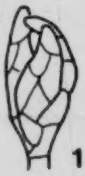
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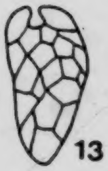
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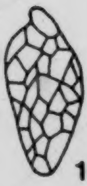
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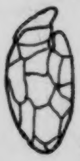
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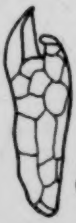
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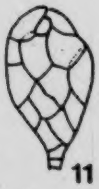
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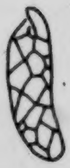
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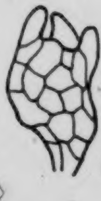
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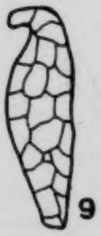
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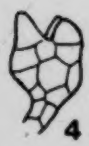
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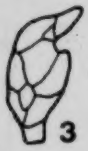
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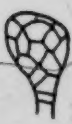
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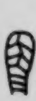
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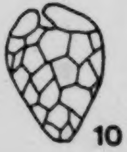

10

FIGURE 51. Scatter diagram comparing *Pohlia annotina* (Hedw.) Lindb. and *Pohlia andrewsii* J. Shaw with respect to propagulum body length and leaf primordium length.

▲= plants with glossy leaves *(P.andrewsii)*
●= plants with dull leaves *(P.annotina)*

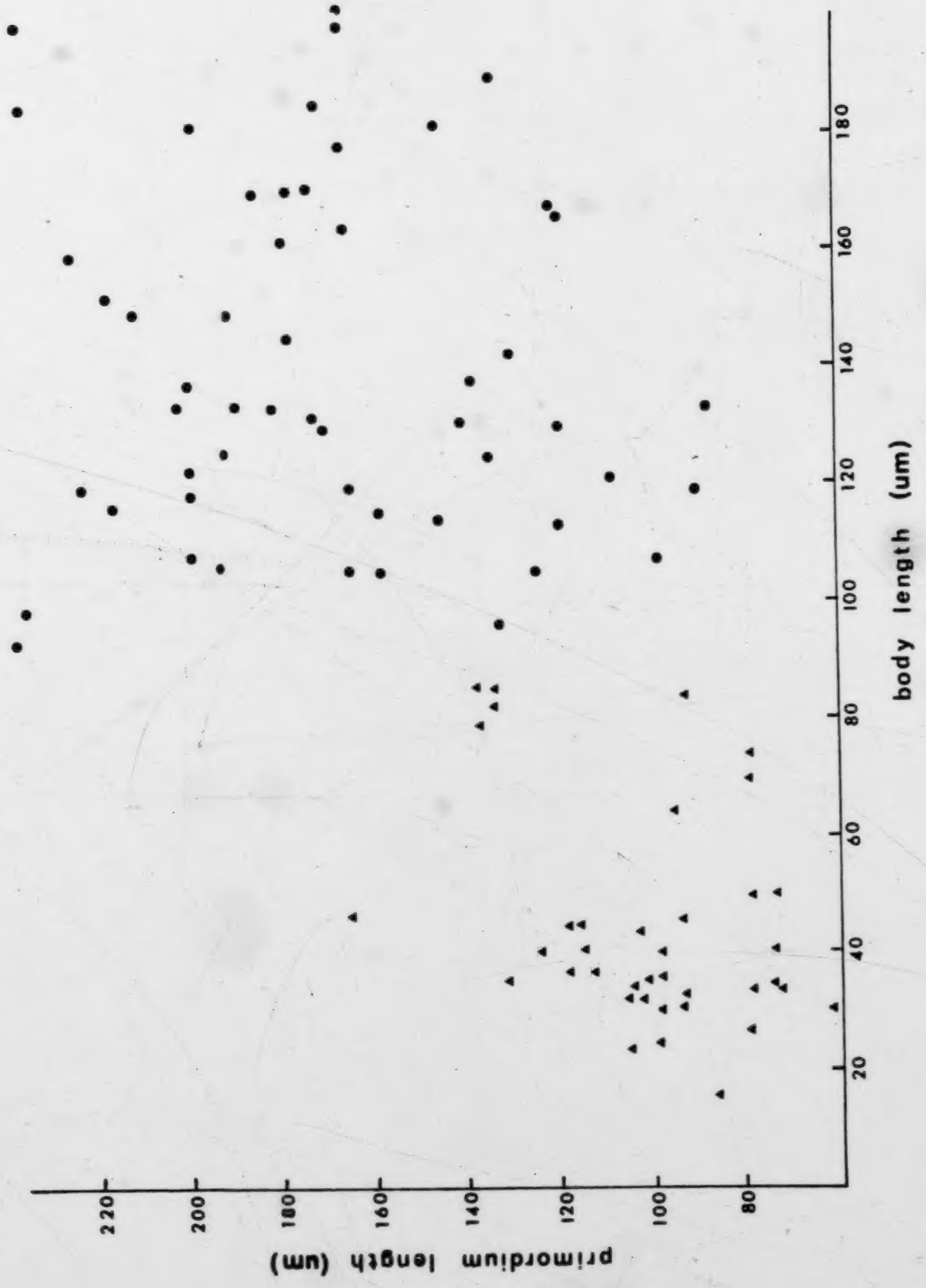
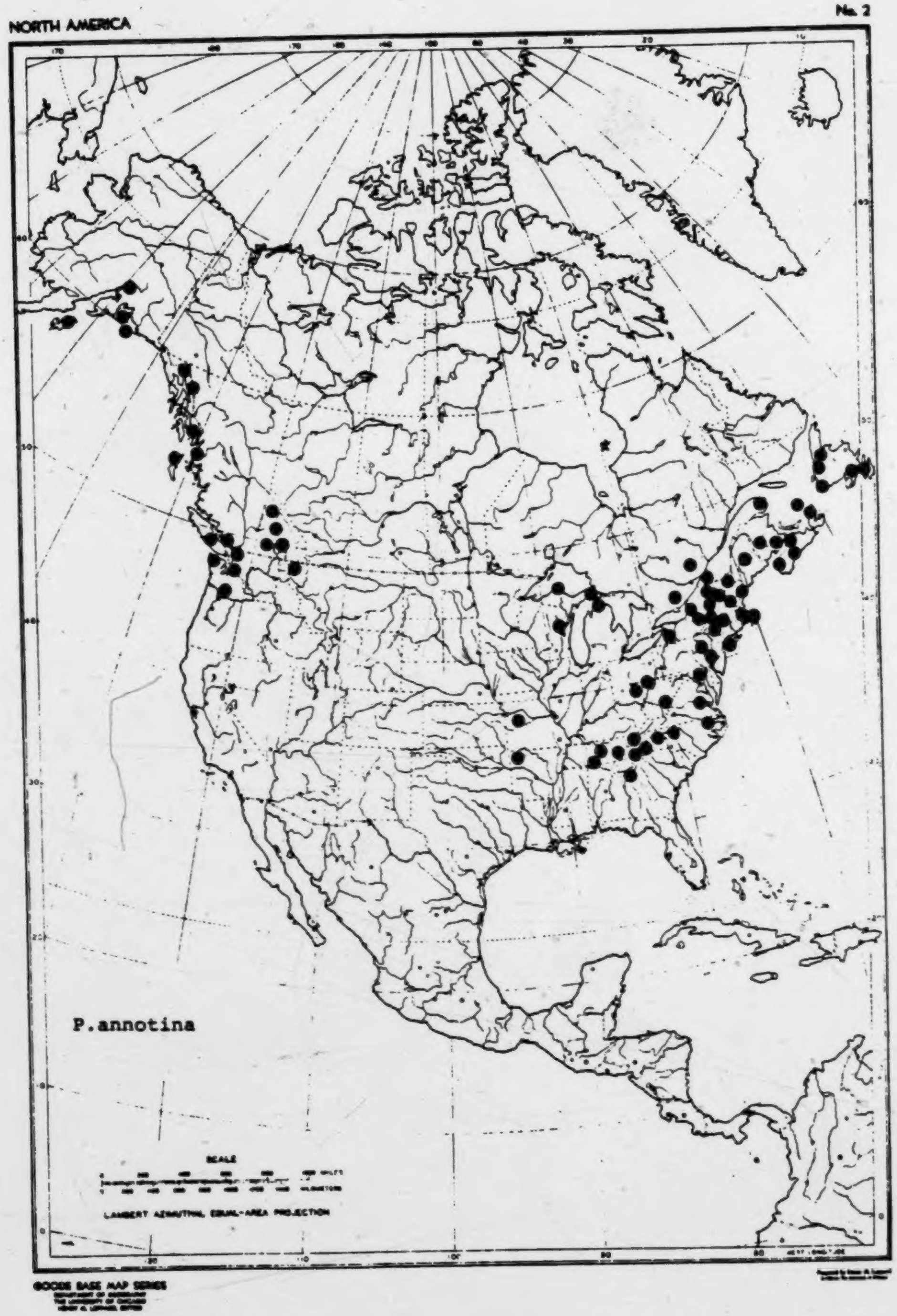

primordium length (um)
220
200
180
160
140
120
100
80
body length (um)
20
40
60
80
100
120
140
160
180

FIGURE 52. *Pohlia annotina* (Hedw.) Lindb., geographic distribution.


NORTH AMERICA
No. 2
P.annotina
SCALE
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GOODE BASE MAP SERIES

FIGURE 53. *Pohlia annotina* (Hedw.) Lindb.

1-10	Stem leaves from just below apex (x36)
11	Perichaetial leaf (x36)
12	Upper leaf cells (x390)
13	Exothecial cells (x390)
14	Costa, transverse section (x390)
15	Capsule, moist (x12)
16	Capsule, dry (x12)
17,18	Perigonial plants (x10)

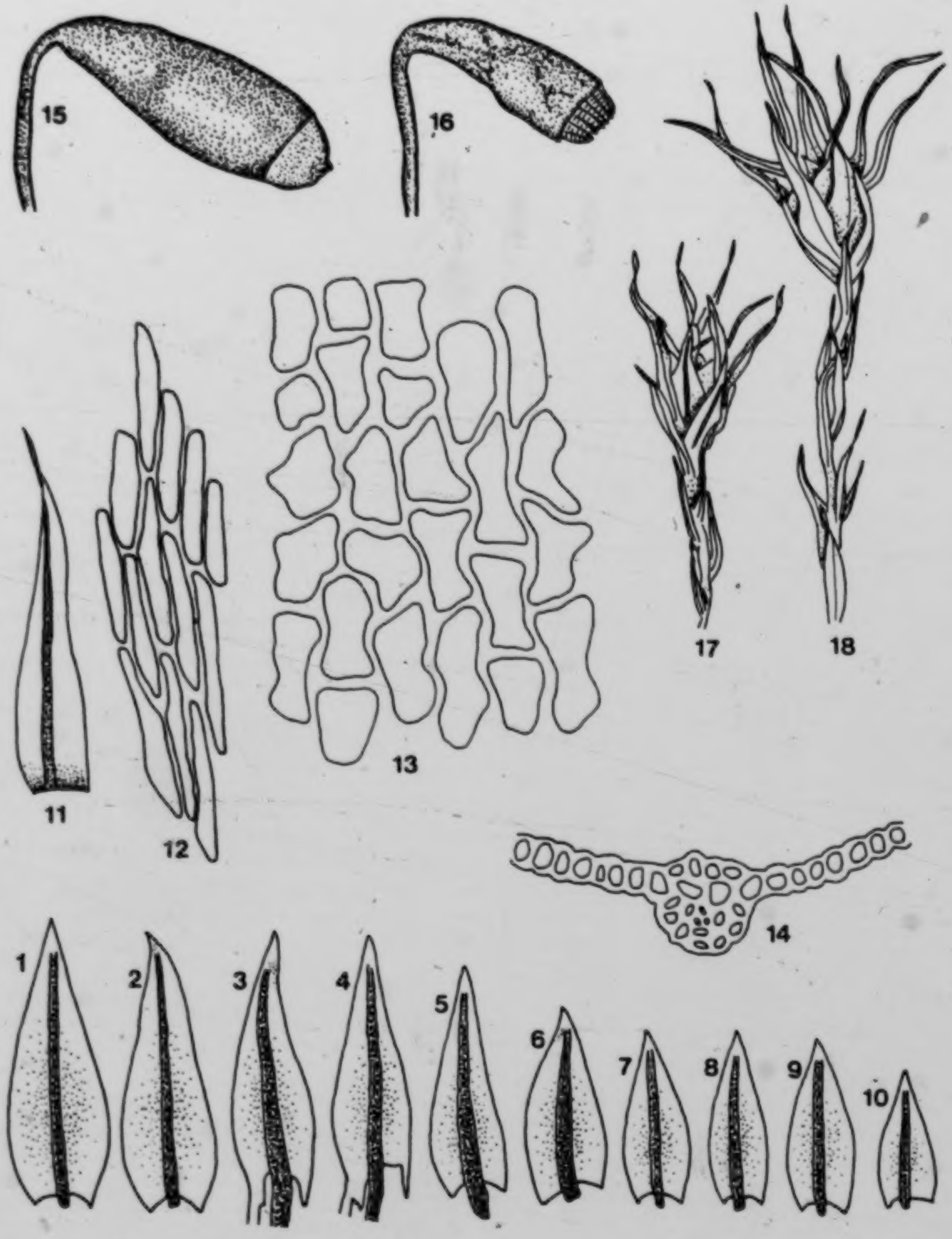


FIGURE 54. *Pohlia annotina* (Hedw.) Lindb., propagula (x280)

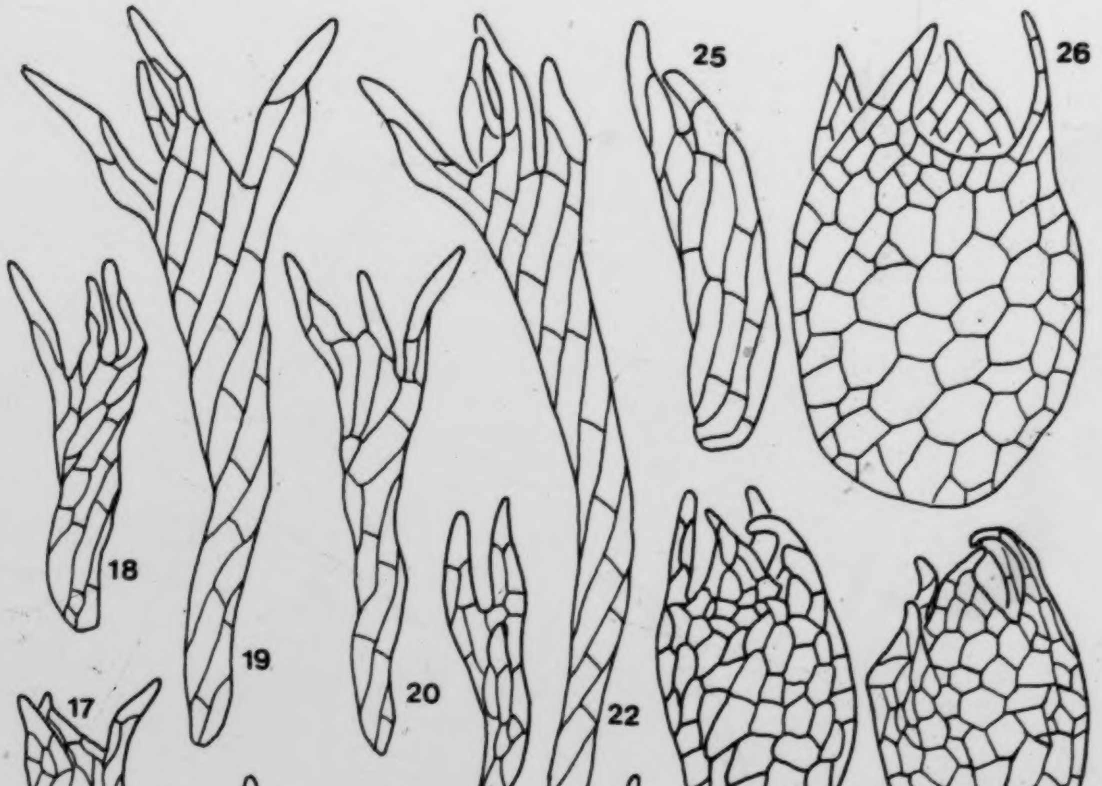


FIGURE 55. Scatter diagram comparing *Pohlia proligera* (Lindb. *ex* Breidl.) Lindb. *ex* Arn. and *Pohlia annotina* (Hedw.) Lindb. with respect to propagulum body width and leaf primordium length. Integers represent the number of leaf primordia and are derived from the mean value for 10 propagula from a population, rounded to the nearest whole number. Circled integers represent values from cultured populations.
Shaded = plants with glossy leaves *(P. proligera)*
Unshaded = plants with dull leaves *(P. annotina)*

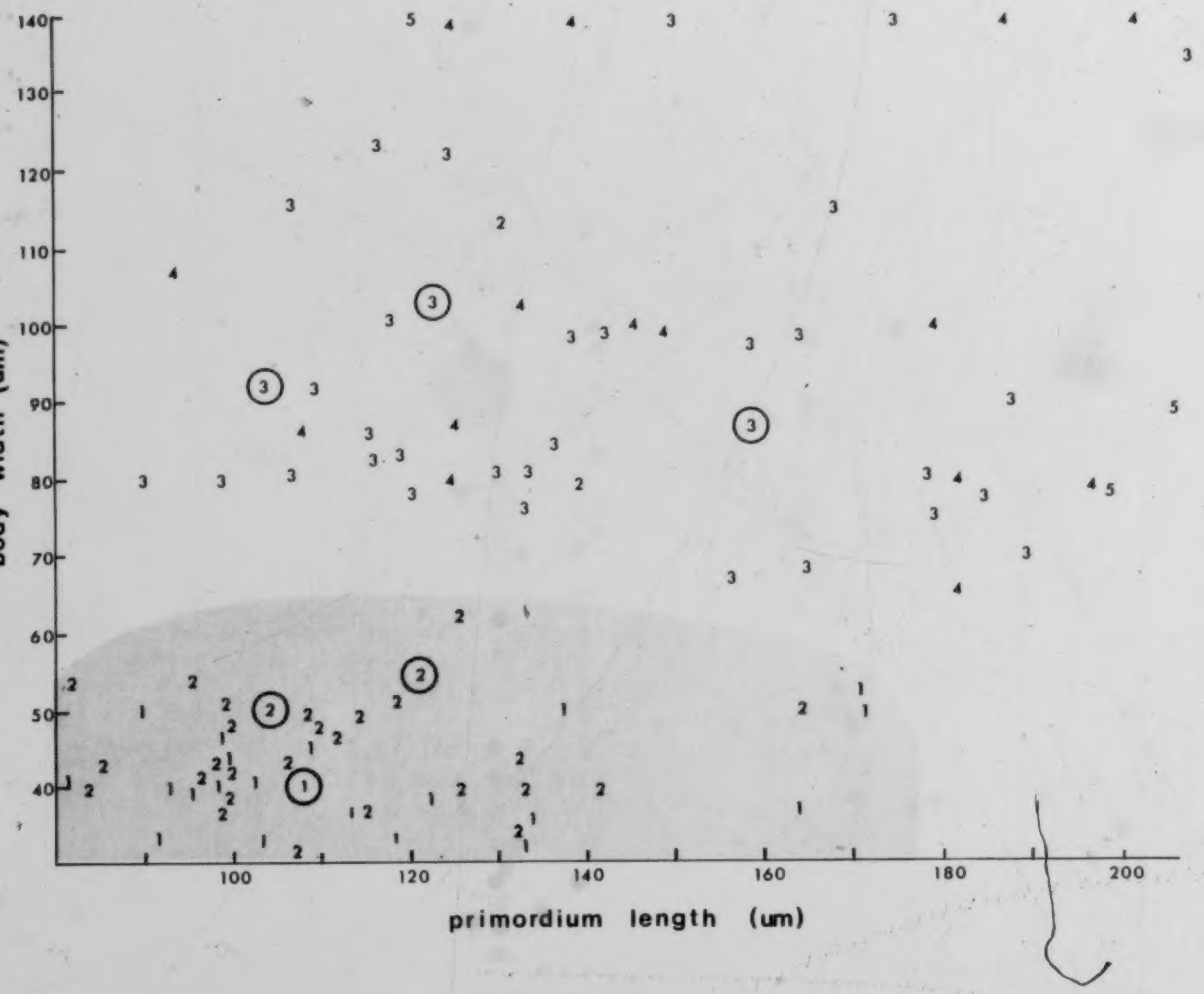
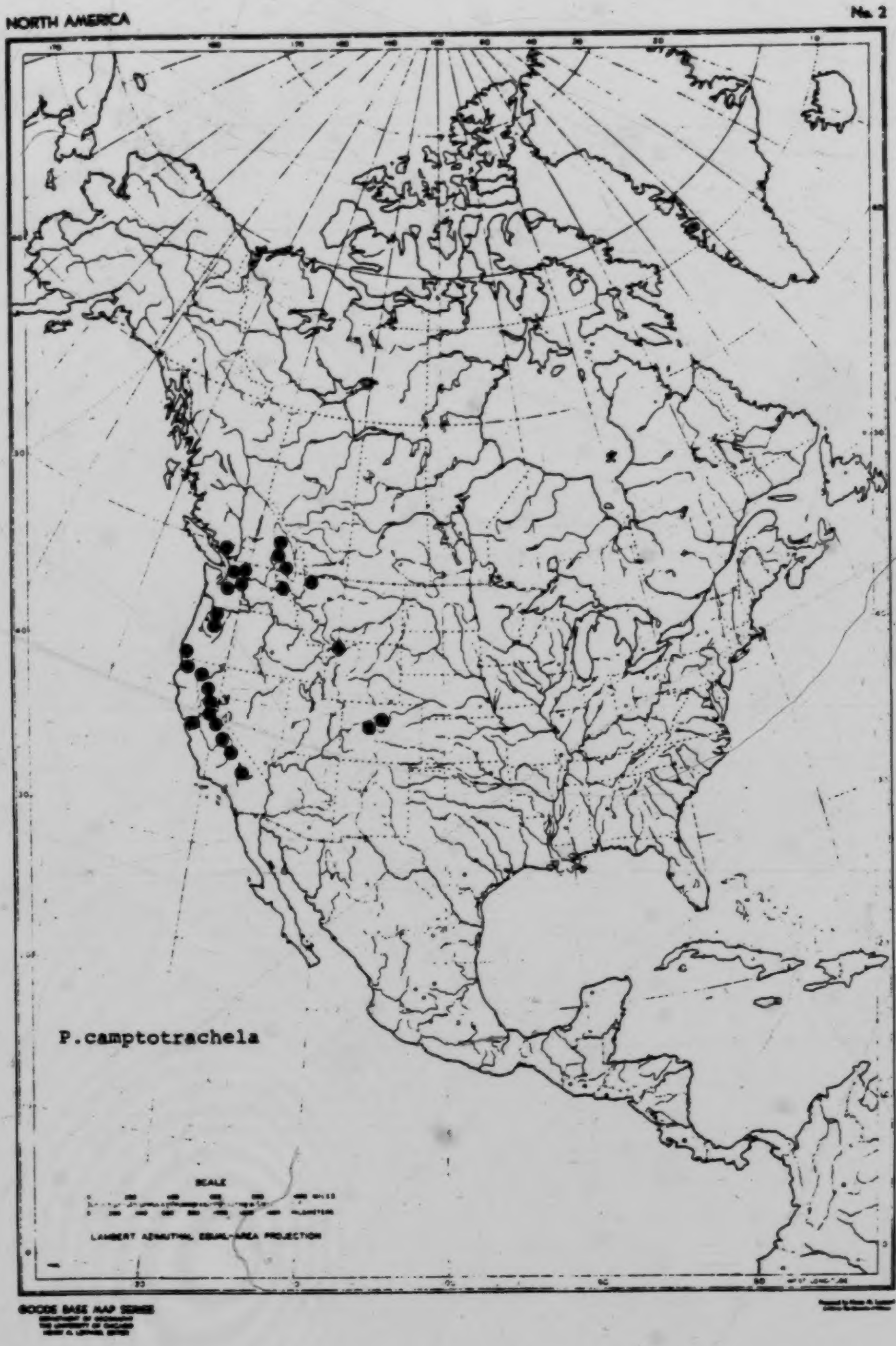

body width (um)
140
130
120
110
100
90
80
70
60
50
40
primordium length (um)
100
120
140
160
180
200

FIGURE 56. *Pohlia camptotrachela* (Ren. & Card.) Broth., geographic distribution


NORTH AMERICA
No. 2
SCALE
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
GOODE BASE MAP SERIES

P.camptotrachela

FIGURE 57. *Pohlia camptotrachela* (Ren. & Card.) Broth.

1-9 Stem leaves from near apex (x36)
10 Perichaetial leaves (x36)
11 Exothecial cells (x390)
12 Upper leaf cells (x390)
13 Costa, transverse section (x390)
14 Capsule, moist (x12)
15 Capsule, dry (x12)
16,17 Perigonial plants (x10)

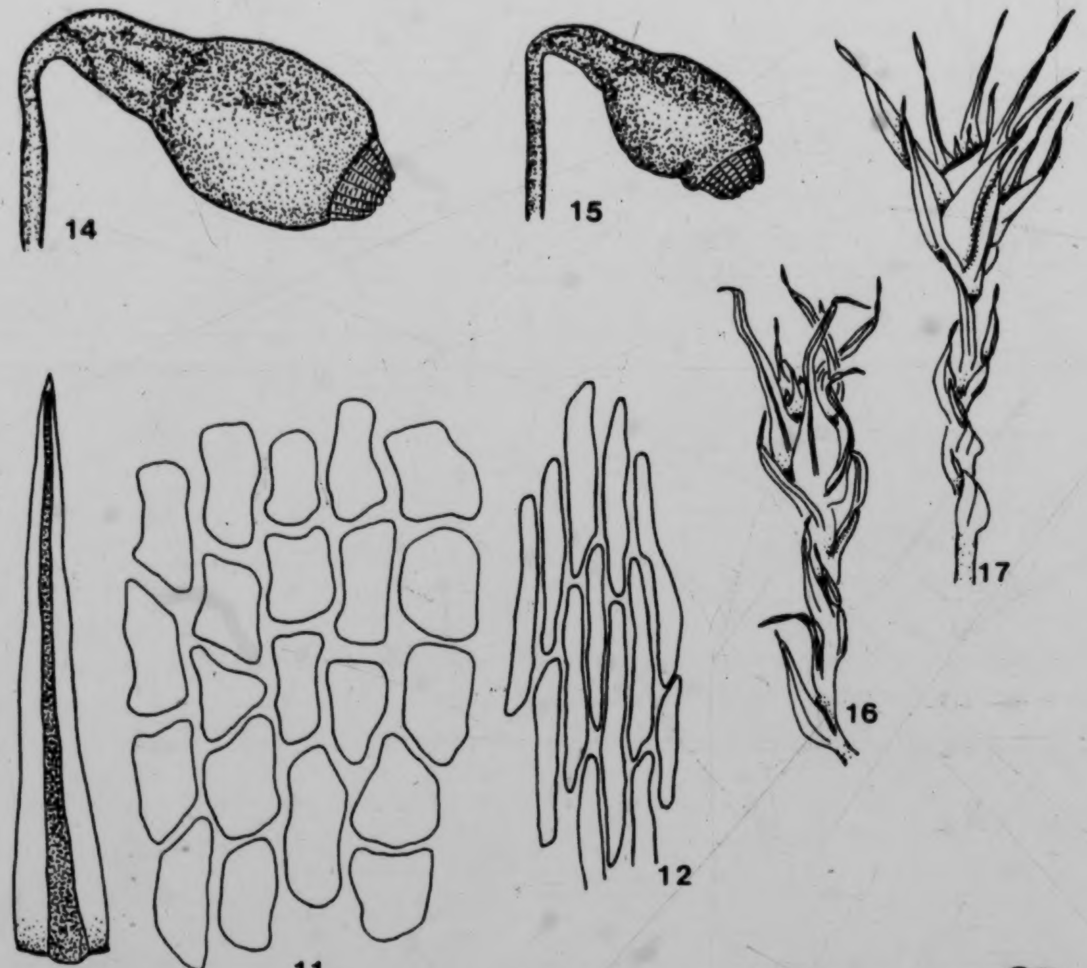


FIGURE 58. *Pohlia camptotrachela* (Ren. & Card.) Broth., propagula (x288)

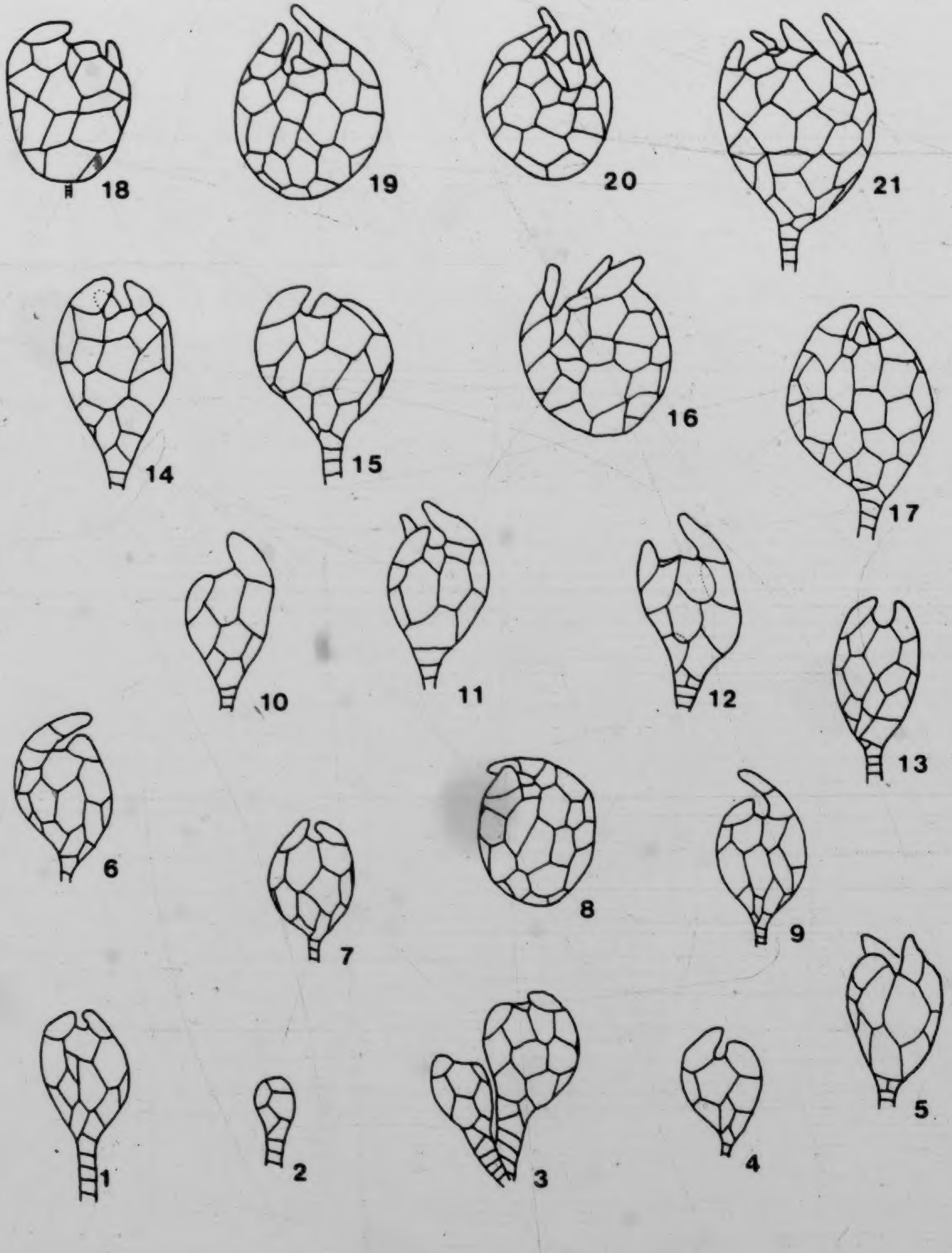


FIGURE 59. Scatter diagram comparing *Pohlia annotina* (Hedw.) Lindb. and *Pohlia camptotrachela* (Ren. & Card.) Broth. with respect to propagulum body length/width and leaf primordium length. Integers represent number of cells constituting the base of leaf primordia, and are derived from the mean value for 10 propagula from a population, rounded to the nearest whole number.
Note the greater scatter of points for *P. annotina*, reflecting its morphological variability.

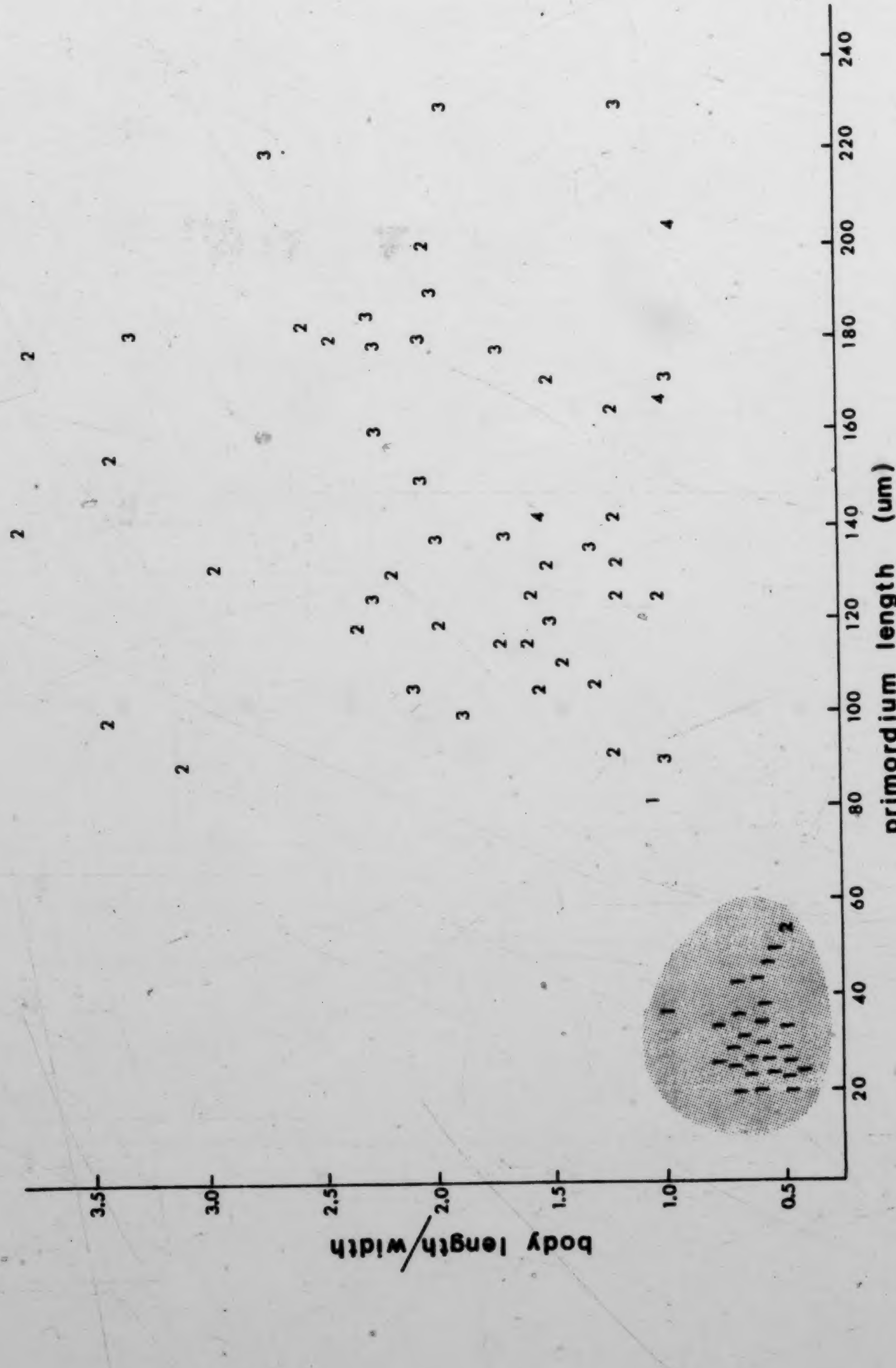
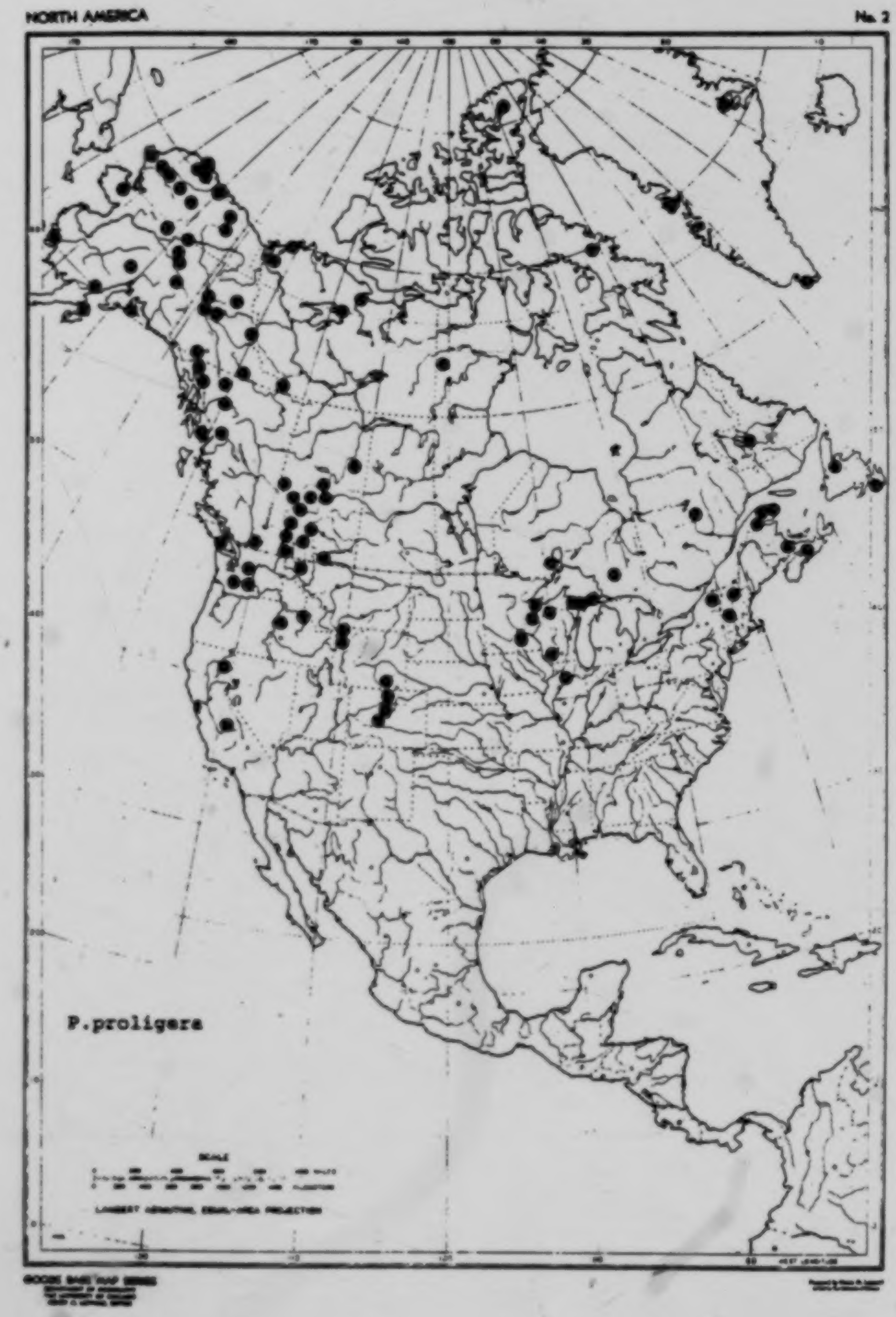

body length/width
3.5
3.0
2.5
2.0
1.5
1.0
0.5
20
40
60
80
100
120
140
160
180
200
220
240
primordium length (um)
2

FIGURE 60. *Pohlia proligera* (Lindb. *ex* Breidl.) Lindb. *ex* Arn., geographic distribution



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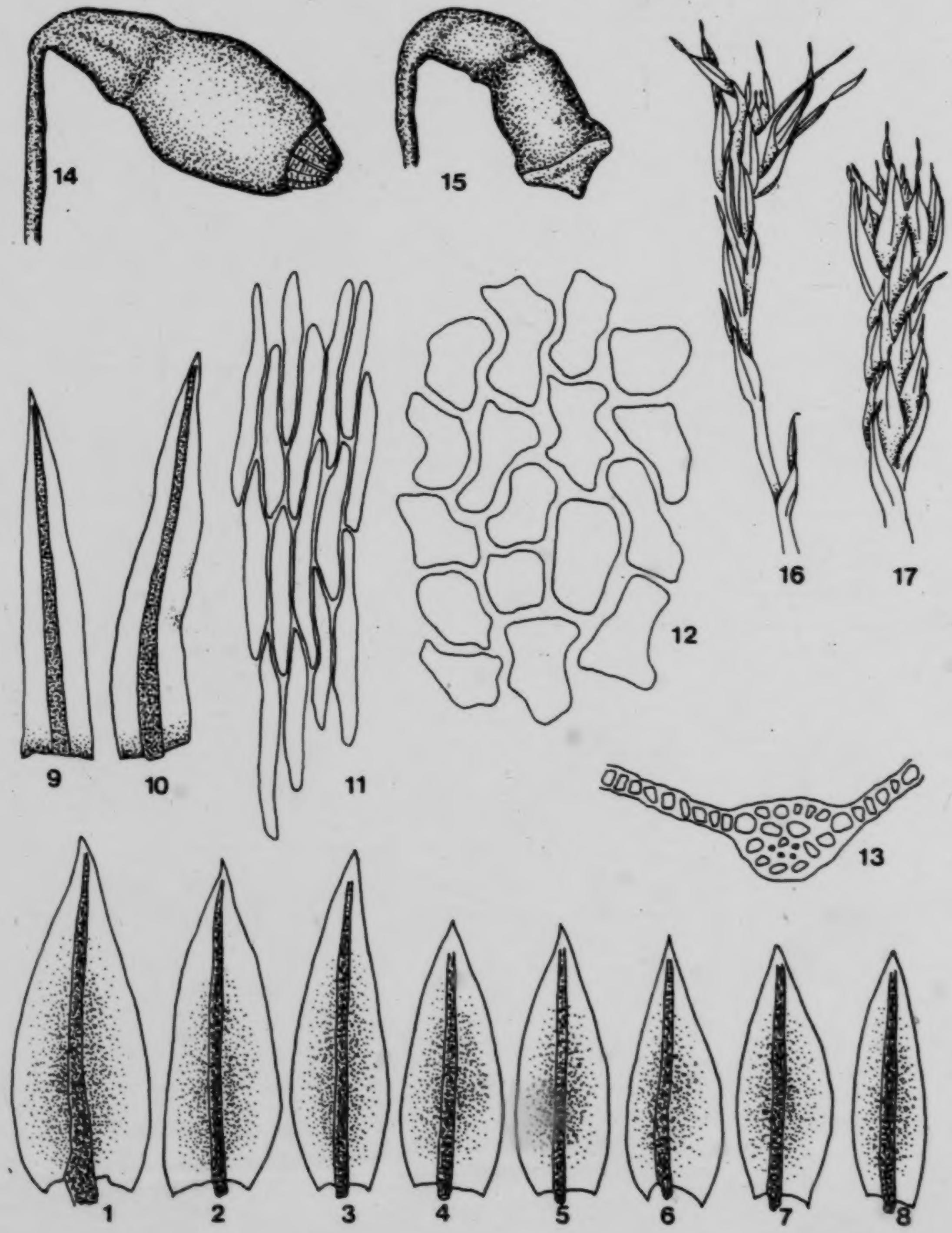
GOODE BASE MAP SERIES

P.proligera

FIGURE 61. *Pohlia proligera* (Lindb. *ex* Breidl.) Lindb. *ex* Arn.

1-8	Stem leaves from just below apex (x36)
9,10	Perichaetial leaves (x36)
11	Upper leaf cells (x390)
12	Exothecial cells (x390)
13	Costa, transverse section (x390)
14	Capsule, moist (x12)
15	Capsule, dry (x12)
16,17	Perigonial plants (x10)



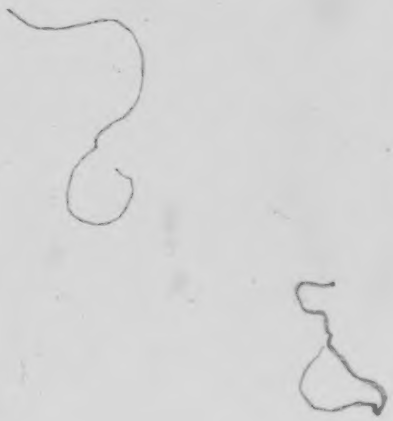


FIGURE 62. *Pohlia proligera* (Lindb. *ex* Breidl.) Lindb. *ex* Arn., propagula (x288)

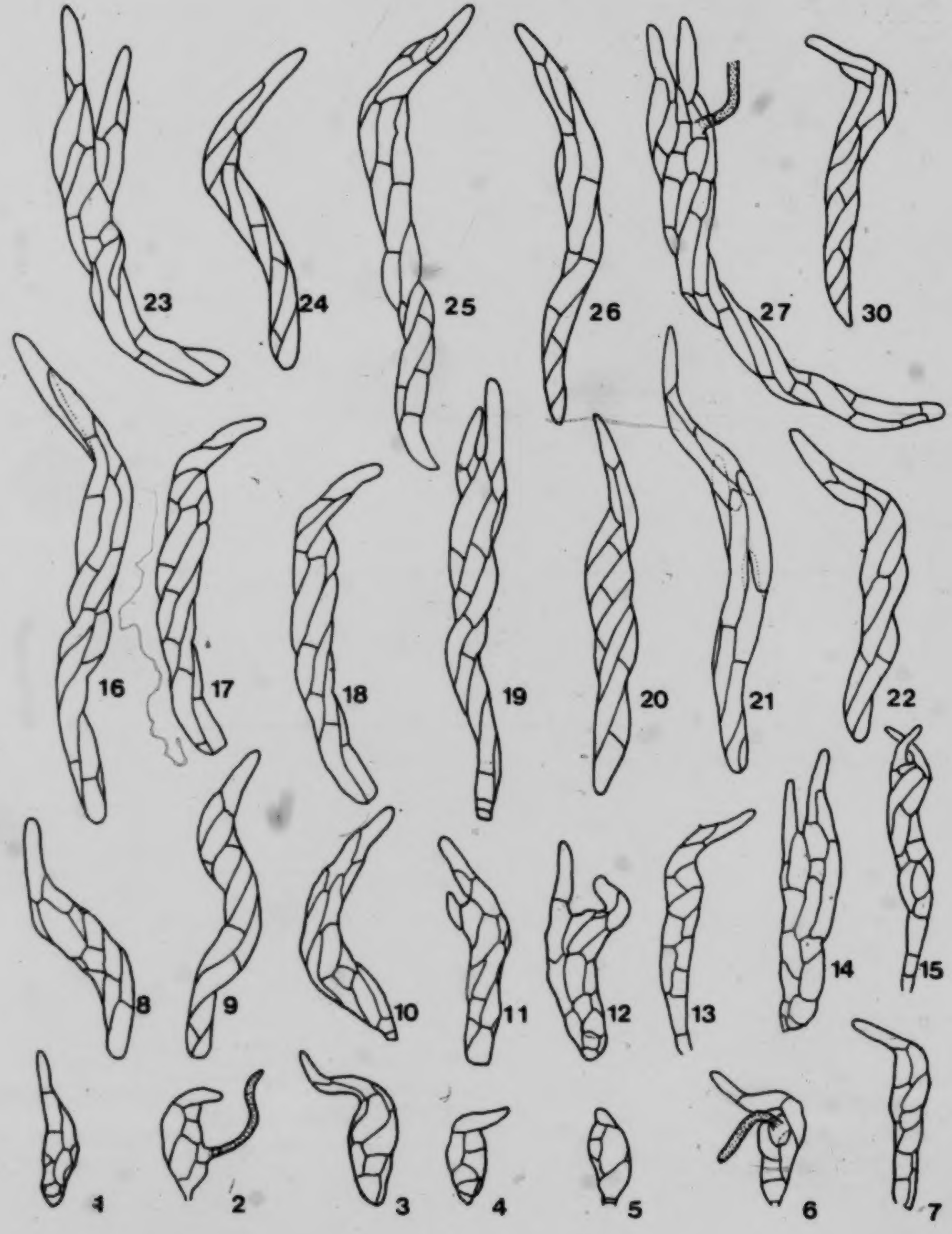
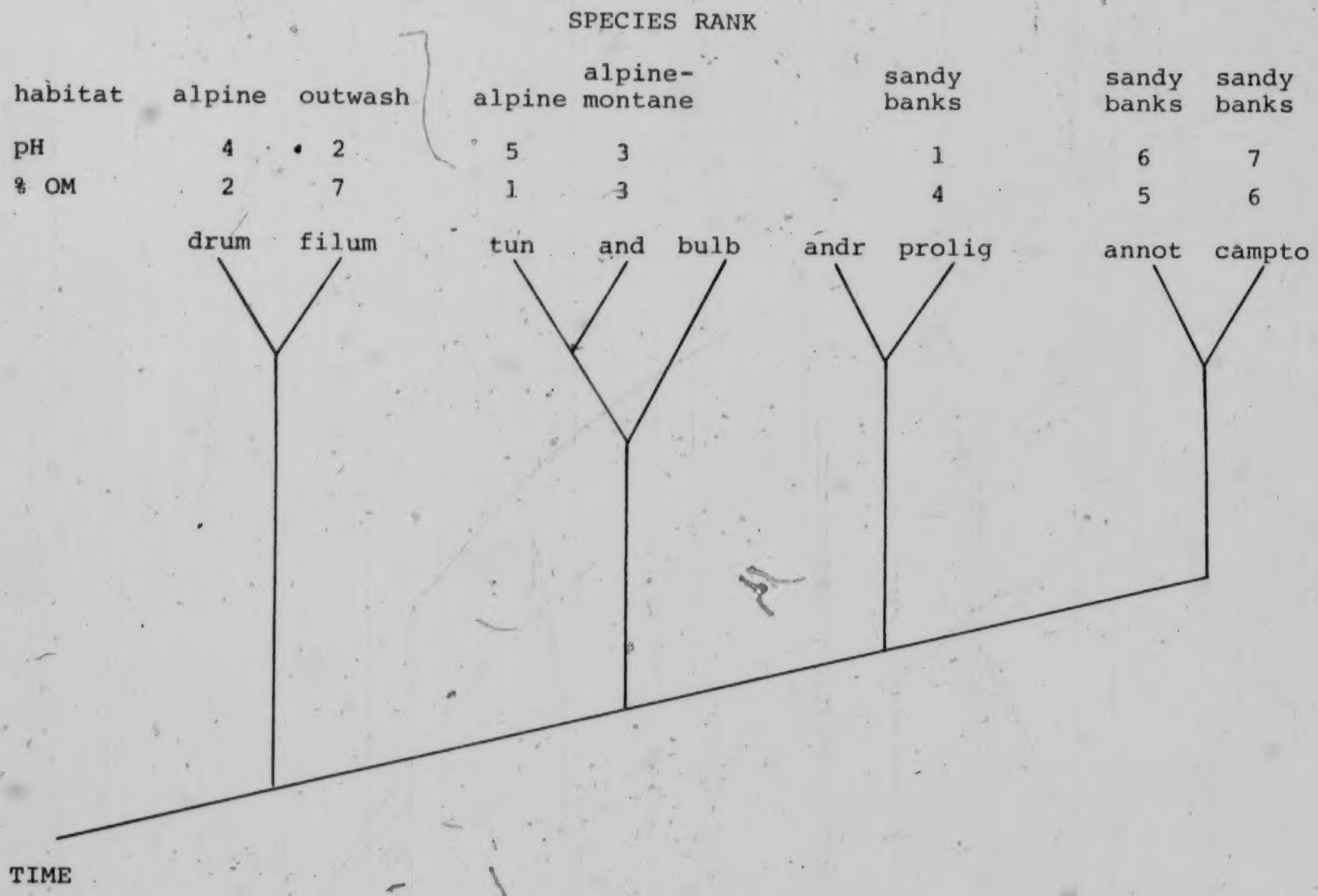


FIGURE 63. Phylogenetic arrangement of the propaguliferous Pohlias. Integers represent species rank along the two ecological gradients. % OM = % organic matter content. 1 = the highest mean % organic matter, 7 = the lowest mean % organic matter. pH = hydrogen ion concentration. 1 = the highest mean pH, 7 = the lowest mean pH. drum = *P. drummondii*, filum = *P. filum*, tun = *P. tundrae*, and = *P. andalusica*, bulb = *P. bulbifera*, andr = *P. andrewsii*, prolig = *P. proligera*, annot = *P. annotina*, campto = *P. camptotrachela*.


SPECIES RANK
habitat
alpine
outwash
alpine
alpine-montane
sandy banks
sandy banks
sandy banks
pH
4
2
5
3
1
6
7
% OM
2
7
1
3
4
5
6
drum
filum
tun
and
bulb
andr
prolig
annot
campto
TIME